

<https://helda.helsinki.fi>

Exploring phylogeny of the microsoroid ferns (Polypodiaceae) based on six plastid DNA markers

Chen, Chi-Chuan

2020-02

Chen , C-C , Hyvönen , J & Schneider , H 2020 , ' Exploring phylogeny of the microsoroid ferns (Polypodiaceae) based on six plastid DNA markers ' , Molecular Phylogenetics and Evolution , vol. 143 , 106665 . <https://doi.org/10.1016/j.ympev.2019.106665>

<http://hdl.handle.net/10138/321115>

<https://doi.org/10.1016/j.ympev.2019.106665>

cc_by_nc_nd

acceptedVersion

Downloaded from Helda, University of Helsinki institutional repository.

This is an electronic reprint of the original article.

This reprint may differ from the original in pagination and typographic detail.

Please cite the original version.

Journal Pre-proofs

Exploring phylogeny of the microsoroid ferns (Polypodiaceae) based on six plastid DNA markers

Chi-Chuan Chen, Jaakko Hyvönen, Harald Schneider

PII: S1055-7903(19)30390-2

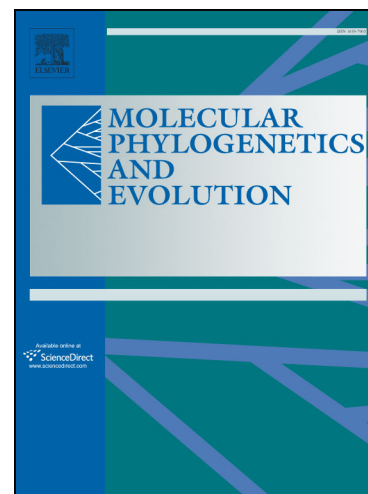
DOI: <https://doi.org/10.1016/j.ympev.2019.106665>

Reference: YMPEV 106665

To appear in: *Molecular Phylogenetics and Evolution*

Received Date: 27 June 2019

Revised Date: 25 October 2019



Please cite this article as: Chen, C-C., Hyvönen, J., Schneider, H., Exploring phylogeny of the microsoroid ferns (Polypodiaceae) based on six plastid DNA markers, *Molecular Phylogenetics and Evolution* (2019), doi: <https://doi.org/10.1016/j.ympev.2019.106665>

This is a PDF file of an article that has undergone enhancements after acceptance, such as the addition of a cover page and metadata, and formatting for readability, but it is not yet the definitive version of record. This version will undergo additional copyediting, typesetting and review before it is published in its final form, but we are providing this version to give early visibility of the article. Please note that, during the production process, errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

Cover Page

Exploring phylogeny of the microsoroid ferns (Polypodiaceae) based on six plastid DNA markers

Corresponding author :

Full name: Harald Schneider

Mail address: Center for Integrative Conservation, Xishuangbanna Tropical Botanical Garden; Chinese Academy of Sciences; Mengla, Yunnan 666303; China

E-mail address: harald@xtbg.ac.cn

Number of tables: 5

Number of black-and-white figures: 5

Declarations of interest: none

Exploring phylogeny of the microsoroid ferns (Polypodiaceae) based on six plastid DNA markers

Chi-Chuan Chen^{1,2}, Jaakko Hyvönen¹, and Harald Schneider^{2,*}

¹ *Organismal & Evolutionary Biology, Viikki Plant Science Center & Finnish Museum of Natural History (Botany), PO Box 7, FI-00014 University of Helsinki, Finland;*

² *Center for Integrative Conservation, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences; Mengla, Yunnan 666303; China;*

*Corresponding author; e-mail: harald@xtbg.ac.cn

ABSTRACT:

The microsoroid ferns are one of the largest subfamilies of the Polypodiaceae with over 180 species mainly found in the humid forests of tropical Australasia. The phylogenetic relationships are still unclear, especially the delimitation of the genus *Microsorium* which has been recognized to be non-monophyletic. We analysed the microsoroid ferns using six chloroplast DNA regions (*rbcL*, *rps4+rps4-trnS*, *trnL+trnL-trnF*, *atpA*, *atpB* and *matK*) in order to present a robust hypothesis of their phylogeny. Our results suggest that they comprise up to 17 genera; of them, 12 agree with a previously accepted generic classification. Five tribes are proposed based on the phylogenetic relationships. Most of the species traditionally included in the genus *Microsorium* are found in six genera belonging to two tribes. In addition to the commonly used DNA markers, the additional *atpA* and *matK* are helpful to provide information about the phylogenetic relationships of the microsoroid ferns.

KEYWORDS:

microsoroid ferns; phylogeny; Polypodiaceae; *matK*; *atpA*

INTRODUCTION

The microsoroid ferns is the third largest out of the six subfamilies of Polypodiaceae containing ca. 12 genera and over 180 species (PPG I, 2016). The lineage is widely distributed in the tropical and subtropical regions of the Old World and Oceania with the range reaching from Japan to Australia and New Zealand, and from Africa, Madagascar, through South and Southeast Asia to South Pacific islands. The microsoroid ferns can be found in terrestrial, epipetric, and rheophytic habitats, as well as growing as epiphytes. The majority of species are usually found in forests with high precipitation, or in habitats close to the water.

There are different opinions regarding the taxonomy of the microsoroid ferns since the morphological similarity and disparity do not reflect well the delimitation (e.g. Hetterscheid & Hennipman, 1984; Bosman, 1991; Nooteboom, 1997). Various authors have proposed several related genera within the microsoroid ferns based on the morphological differences (Table 4). However, with later studies incorporating molecular data, many of these genera were subsequently merged (Wang et al., 2010b; Kim et al., 2013; Wei et al, 2017). The latest classification PPG I (2016) accepted 12 genera within the microsoroid ferns treated as a subfamily. In addition to *Microsorium* Link, *Goniophlebium* (Blume) C. Presl, *Lecanopteris* Reinw. ex Blume, *Lemmaphyllum* C. Presl, *Lepidomicrosorium* Ching & K.H.Shing, *Lepisorus* (J.Sm.) Ching, *Leptochilus* Kaulf., *Neocheiropteris* H. Christ, *Neolepisorus* Ching, *Paragramma* (Blume) T. Moore, *Thylacopteris* Kunze ex J. Sm., and *Tricholepidium* Ching are currently accepted. However, the previous studies also pointed out that *Microsorium* s.l. is a paraphyletic unit that requires further attention. (e.g. Kreier et al., 2008; PPG I, 2016).

Various classifications have been presented above the generic level. Hennipman et al. (1990) suggested two subfamilies and six tribes within Polypodiaceae, the microsoroid ferns being tribe Microsoreae containing eight genera, *Christiopteris* Copel., *Dictymia* J. Smith, *Colysis* C. Presl, *Lecanopteris*, *Leptochilus*, *Microsorium*, *Neocheiropteris*, and *Phymatosorus* Pic.Serm. The morphological characters of this tribe include leaves that are simple or variously dissected, leaf indument such as scales and/or hairs, spore exospore usually thin and perispore is variable, as well as stem scales usually clathrate. Among these eight genera, the last six are accepted as the microsoroid ferns in the latest classification PPG I with *Colysis* included within *Leptochilus*, but the Australian species of *Colysis* have been placed in another clade (Testo & Sundue, 2014). *Christiopteris* and *Dictymia* have been placed in the subfamilies Drynarioideae and Loxogrammoideae, respectively (PPG I, 2016). The subdivision of Hennipman et al. (1990) provides a preliminary classification of the microsoroid ferns, but is still treated as provisional and likely artificial (Schneider et al., 2004b).

With the studies based on DNA sequences during the past decade, the phylogenetic relationships of the microsoroid ferns have also been assessed not only locally (Schneider et al., 2004a, 2006; Kim et al., 2013), but also on a global scale (Schneider et al., 2004b; Kreier et al., 2008; Nitta et al., 2018). Based on plastid DNA markers, the microsoroid ferns appear to be monophyletic, but some traditional genera such as *Microsorium* and *Phymatosorus* were found to be paraphyletic or polyphyletic (Bosman, 1991; Schneider et al., 2004b; Kreier et al., 2008; PPG I, 2016). The deeper relationships of the microsoroid ferns including tribes Microsoreae, Polypodieae, and Lepisoreae as presented by Hennipman et al. (1990) were studied by Kreier et al. (2008) using four chloroplast regions (*rbcL*, *rps4*, *rps4-trnS* IGS, and *trnL-trnF* IGS) from 107 samples of 87 species. Six groups were described: membranaceoid, lecanopteroid, lepisoroid, microsoroid s.s., thylacoperoid, and goniophleboid clades, with the first four clades belonging to the core microsoroids. Some of the clades were subsequently studied more to clarify the classification, such as the lepisoroid clade (Wang et al., 2010a, 2010b) following the tribal ranking of Hennipman et al. (1990), *Leptochilus* which is part of the microsoroid s.s. clade (Zhang et al., 2019), and in light of the recent study lecanopteroid ferns (Testo et al., 2019). One of the reasons for morphological similarity between species of the microsoroid ferns is hybridization, with many hybrid species reported (Nooteboom, 1997; Fraser-Jenkins, 2008; Nitta et al., 2018; Zhang et al., 2019), especially within the microsoroid s.s. clade of Kreier et al. (2008). This makes generic delimitation difficult in some cases (Nitta et al., 2018). There are still many relationships to be solved within the microsoroid ferns although the main groups have been delimited (Kreier et al., 2008; Nitta et al., 2018). In this study, we assembled a comprehensive taxon sampling from all 12 genera as defined in PPG I (2016), with six sampled chloroplast regions. Of them, markers *matK* and *atpA* are used for the first time in phylogenetic analysis of this group. We aimed to reevaluate the phylogeny with a focus on higher ranks, in order to provide a robust classification of this fern group.

MATERIAL AND METHODS

Taxon sampling

The taxa were sampled (Table 1) to capture a wide range of variation of microsoroid diversity, containing the type species of all previously proposed genera whenever possible (Table 4). The circumscriptions of the genera used in this study mainly follow PPG I (2016) with 12 genera accepted, including *Lepidomicrosorium*, *Leptochilus*, *Microsorium*, *Neocheiropteris*, *Neolepisorus*, *Thylacopteris*, *Goniophlebium*, *Lecanopteris*, *Lemmaphyllum*, *Lepisorus*, *Tricholepidium*, and *Paragramma*. Of these, the sequences for the first six genera were mainly generated in this study, while the

sequences of the last six were mostly from previous studies and thus downloaded from GenBank. In total, 316 terminals were included representing 155 species (Table 1). The species *Aglaomorpha meyeniana* Schott, *Polypodium glycyrrhiza* D.C. Eaton, and *Pyrrosia polydactyla* (Hance) Ching were chosen as outgroup terminals based on their close relationship with the microsoroid ferns (PPG I, 2016).

Material for generating DNA sequences were collected from the wild, herbarium specimens, or from plants cultivated either in the Xishuangbanna Tropical Botanical Garden (XTBG) or the Koo Botanic Conservation Center (KBCC). Voucher specimens of the newly collected specimens were deposited in the herbarium (HITBC) of Xishuangbanna Tropical Botanical Garden of Chinese Academy of Sciences, and the Botanical Museum of the University of Helsinki (H). Altogether 438 novel sequences were generated in this study.

Extraction, amplification, and sequencing

For each sample, genomic DNA was extracted from ca. 20 mg of silica-dried leaves by using EasyPure® Plant Genomic DNA Kit (Beijing, China). The extracts were used directly for PCR amplification with the various primers (Table 2). The PCR reactions were performed in a 50 µl volume containing >20 ng genomic DNA, 5 µl 10x EasyTaq buffer, 4 µl dNTP solution (2.5 mM), 1 µl of each primer (10 µM), and 0.5 µl EasyTaq DNA Polymerase. We chose six DNA regions to be used: *rbcL*, *rps4+rps4-trnS* (*rps4* gene and *rps4-trnS* intergenic spacer), *trnL+trnL-trnF* (*trnL* intron and *trnL-trnF* intergenic spacer), *atpB*, *atpA* and *matK*. The three regions listed first were used in the earlier studies (e.g. Schneider et al., 2004b, 2006; Kreier et al., 2008; Wang et al., 2011). Also *atpB* and *rbcL-atpB* have been used previously (Wang et al., 2010a, 2010b; Kim et al., 2013; Wei et al., 2017; Zhang et al., 2019). The latter two, *atpA* and *matK*, were used for the first time for the microsoroid ferns in this study. The *matK* region was amplified using primers designed for the CBoL plant Barcode (see CBoL Plant Barcoding Group 2009;

http://api.ning.com/files/BUlqLWUg9ErBrrLy0nYWDNOINjg*fmvyMzVAb4L6oMWusIIos1eJWVNkti4LNRtUgt3IVmhw9YnTKOZhG8EyUeoYpXRWp1xc/Fern_matK_RBGE_PROTOCOLv1.0.pdf).

Sequence alignment and phylogenetic analysis

The DNA strands were assembled and edited using BioEdit (Hall, 1999) and aligned using MUSCLE (Edgar, 2004) within Mesquite 3.31 (Maddison & Maddison, 2017). The obtained alignments were checked visually for ambiguously aligned regions that were subsequently excluded. In addition, the sequences of *rbcL-atpB* from GenBank were merged with *atpB* since it was available for most of the taxa, especially *Lepisorus*,

Lemmaphyllum, and *Lepidomicrosorium*. In total, we obtained 308 sequences for *rbcL*, 310 for *rps4 + rps4-trnS*, 302 for *trnL+trnL-trnF* regions, 185 for *rbcL-atpB + atpB*, 62 for *atpA*, and 51 for *matK*. The novel sequences were deposited in GenBank (see Table 1 for accession numbers).

We compiled four concatenated datasets, three of them were large containing all 316 taxa but the combined DNA regions differed: 1) concatenated dataset of all six DNA regions of 316 samples, with *atpA* and *matK* regions lacking for most of the terminals; 2) concatenated dataset of four DNA regions (*rbcL*, *rps4 + rps4-trnS*, *trnL+trnL-trnF*, and *rbcL-atpB + atpB*), with *rbcL-atpB + atpB* available only for part of the terminals; and 3) concatenated dataset of three regions (*rbcL*, *rps4 + rps4-trnS*, and *trnL+trnL-trnF*) with relatively complete representation of all the terminals. These three combinations of large datasets were analysed to assess whether and how much different number of terminals and available sequences affect obtained topologies. The fourth concatenated dataset was small and designed to further check the obtained phylogenetic structure. It contained 50 taxa representing all 12 genera, with data of all six regions.

Maximum Likelihood analyses (ML) were performed using IQ-Tree 1.5.6 (Nguyen et al., 2015), and Bayesian Inference (BI) using MrBayes v. 3.2.6 (Ronquist and Huelsenbeck, 2003). The partitionFinder (Lanfear et al., 2016) was used for both ML and BI analyses. For ML, ModelFinder (Kalyaanamoorthy et al., 2017) was used to identify the best fitting model for these analyses which was implemented in IQ-Tree 1.5.6. (Nguyen et al., 2015). Bayesian Information Criterion (BIC) was selected for all datasets, and the best fitting models was found for each DNA region separately (Table 3). ML analyses were run simultaneously under default settings with both non-parametric bootstrap analyses using the ultrafast bootstrap (UFBoot; Minh et al., 2013), Shimodaira-Hasegawa-like approximate likelihood ratio test (SH-aLRT; Guindon et al., 2010), and the Bayesian-like transformation of aLRT (aBayes; Anisimova et al., 2011) as implemented in IQ-Tree (Trifinopoulos et al., 2016). The interpretation of the support values employed the criteria following previous publications (e.g. Minh et al., 2013).

For the BI analyses, not only partitioned regions but also the best fitting models were selected using partitionFinder (Lanfear et al., 2016). Markov chain Monte Carlo was run independently twice with one cold and three hot chains. In each run, chains were sampled every 1000 cycles. A total of 10,000,000 generations were run and a majority rule consensus tree was calculated based on all trees sampled except that the first 25% of the sampled trees were discarded within the burn-in phase, which was examined using Tracer v. 1.6 (Rambaut and Drummond, 2007) to ensure convergence of chains and sufficient sampling of generations. The posterior probabilities (PP) were calculated

and presented using the majority rule consensus tree. The published results were based on the concatenated datasets including all regions using the partitioning (Fig. 1, 2). We performed an analysis of the largest dataset with parsimony as an optimality criterion using the program TNT (Goloboff et al., 2008; Goloboff and Catalano, 2016) that provides efficient algorithms for the analyses of large (> 200 taxa) datasets. By including in the analyses also the specimens with only part of the sequences, we wished to see how they affected the results obtained. The pathological behavior of specimens with only part of the characters (Wheeler, 2012) is well known (e.g. Nixon and Davis, 1991; Platnick et al., 1991) but results of several studies (e.g. Lehtonen, 2011; Wolsan and Sato, 2010) suggest that analyses of even sparse matrices are worthwhile. Analyses using TNT were performed with the search settings following the settings used in Wheeler et al. (2017). Initially, parsimony uninformative characters were removed from the matrix using “mop uninformative characters” function of the program Winclada (Nixon, 2002). This resulted in a matrix of 316 terminals and 2184 characters. Searches were initiated with ten replicates of RAS (random addition sequence) + TBR (tree-bisection-reconnection) branch swapping, and this was performed 30 times in order to get a large pool of diverse trees that were already closer to an optimal solution, rather than a sample of random trees. After this, each set of 10–30 trees (trees saved per replicate 1, 2, or 3) obtained were subjected to a new technology search composed of sectorial search (random and mixed sectorial searches) plus tree-drifting (Goloboff, 1999), with default settings. Finally, all trees were combined and subjected to 1000 rounds of tree-fusing (Goloboff, 1999), again using default settings of the program.

RESULTS

The tree topologies resulting from analyses of the three large datasets were generally congruent. In all the topologies, Thylacopterae then Goniophlebidae were successively sister to the core microsoroid ferns which was in turn comprised of Lecanopterae, Microsoreae, and Lepisoreae (Figs. 1, 2, 4). The Microsoreae and Lepisoreae were sister clades to which the Lecanopterae was a sister (Figs. 1, 4). The Lecanopterae (Fig. 1) contained the ant-fern genus *Lecanopteris* and three lineages comprising species of *Microsorium*; two of them, groups MG2 and MG3, contained mostly Australasian species. These two groups plus *Lecanopteris* formed a branch with high bootstrap and posterior values (Fig. 1; aLRT = 100% / aBayes = 1.00 / UFBoot = 100% / PP = 1.00). Together, they were sister of MG1. Microsoreae and Lepisoreae clades comprised the majority of the microsoroid ferns. Of them, Microsoreae consisted of four clades, *Leptochilus*, core *Microsorium*, MG4, and MG5; the majority of the sampled *Microsorium* species were placed in the latter

three clades. The clades MG5 and *Leptochilus* were sister to each other (Fig. 1; aLRT = 99.5% / aBayes = 1.00 / UFBoot = 100% / PP = 1.00) and together were a sister clade of the clades MG4 and core *Microsorium* (Fig. 1; aLRT = 89.9% / aBayes = 1.00 / UFBoot = 99.0% / PP = 1.00). The type species of *Microsorium* (*M. punctatum* (L.) Copel.) and *Phymatosorus* (*M. scolopendria* (Burm. f.) Copel.) were nested in the core *Microsorium* but in different subclades (Fig. 1; Table 4).

There were seven genera in the tribe Lepisoreae and it was divided into three main clades. *Lepisorus* and *Paragramma* were two clades with the rest five genera, *Neolepisorus*, *Lemmaphyllum*, *Tricholepidium*, *Neocheiropteris*, and *Lepidomicrosorium* forming one clade (Fig. 2). Among these *Lemmaphyllum* was separated from the other four genera (Fig. 2; aLRT = 100% / aBayes = 1.00 / UFBoot = 100% / PP = 1.00). *Neolepisorus*, *Tricholepidium*, *Neocheiropteris*, and *Lepidomicrosorium* were monophyletic, with the first one as a sister of the other three. The position of *Paragramma longifolius* (Blume) T. Moore and *Lepisorus accedens* (Blume) Hosok differed among the tree topologies that resulted from the three large datasets. *Paragramma* was sister of *Lepisorus* in the analysis based on four gene regions, or placed as a first branch within Lepisoreae, which was sister of the other six genera in the analyses based on three and six genes regions (Figs. 1, 4). *Lepisorus accedens* was sister to *Lemmaphyllum* in the analysis of three genes (Fig. 4), whereas it was nested within *Lepisorus* in both of the four and six gene region analyses (Figs. 1, 4).

A similar topology was also found in the ML analysis of the small dataset which included *P. longifolius* but without *L. accedens* (Fig. 3). The tribe Lepisoreae was a clade with high support value both in large (Fig. 2; aLRT = 100% / aBayes = 1.00 / UFBoot = 100% / PP = 1.00) and small (Fig. 3; aLRT = 99.9% / aBayes = 1.00 / UFBoot = 100%) dataset analyses, but the node after *P. longifolius* had lower support values in both large and small dataset (Fig. 2; aLRT = 61.9% / aBayes = 0.953 / UFBoot = 93% / PP = 0.997; and Fig. 3; aLRT = 68.2% / aBayes = 0.98 / UFBoot = 79%). The parsimony analysis based on six genes resulted in a similar topology, but the position of *L. accedens* was unresolved; it was a branch of the large polytomy of the Lepisoreae (Fig. 5). The tree is consensus of 1714 equally parsimonious trees with a length of 7677 steps. As can be seen the number of trees was inflated mostly by the conflict in some smaller groups.

DISCUSSION

Our results reveal that the microsoroid ferns can be divided into 17 clades, with aLRT > 97%, aBayes = 1, UFBoot ≥ 99%, and PP = 1; and 12 of these clades are accepted in the generic classification of PPG I (2016). Our results agree with previous studies that

supported traditional *Microsorium* and *Phymatosorus* as being not monophyletic. These species can be found in several clades containing MG1-MG5 plus core *Microsorium*, and thus the delimitation of these genera needs to be reevaluated. In addition, there are five tribes within the microsoroid ferns that are recognized in this study.

The use of *atpA* and *matK* in the phylogenetic analyses of the microsoroid ferns

We analysed three large datasets included different numbers of DNA regions (three, four, and six). Of them, the one with three included the DNA regions *rbcL*, *rps4* + *rps4-trnS*, and *trnL+trnL-trnF* that have been used in previous phylogenetic studies of microsoroid ferns (e.g. Kreier et al., 2008). The one with four regions also include *rbcL-atpB* + *atpB* besides those listed above. This region was used previously to study the phylogenetic relationships of *Lepisorus* species (Wang et al., 2010a). The regions *atpA* and *matK* have been considered to be useful markers for solving the core relationships of ferns (Schuettelpelz et al. 2006; Kuo et al., 2011). Although these two regions were obtained only for small proportion of our samples they were added to the largest dataset.

The trees inferred from the three large concatenated datasets show relatively consistent results, in that there are 17 main groups in all trees, but clades are supported differently among the datasets, especially for the relationships of the core *Microsorium* and MG4. The clades containing these two groups are weakly supported in the three- combination dataset (Fig. 4; aLRT = 51.4% / aBayes = 0.93/ UFBoot = 87.0%), but are better supported in the four-combination (Fig. 4; aLRT = 72.1% / aBayes = 0.99/ UFBoot = 97.0%) and six-combination datasets (Fig. 4; aLRT = 89.9% / aBayes = 1/ UFBoot = 99.0%). These results agree that *atpA* and *matK* improve the resolution of the phylogenetic framework of the microsoroid ferns. Unfortunately, the relationships within Lepisoreae did not improve much among three datasets. This was likely caused by the limited number of sampled species, since most of the *atpA* and *matK* data are from Microsoreae species and only a few are from tribe Lepisoreae (Table 1).

Phylogenetic relationships and the delimitation of tribes of the microsoroid ferns

Our phylogenetic trees are composed of five well-supported branches (Fig. 1 & 2; Fig. 3), and this is congruent with the results obtained in the previous studies (Kreier et al., 2008). In order to make taxonomy useful, suitable ranks within the microsoroid ferns are needed, since it is such a large and diverse fern group. We follow PPG I (2016) that uses subfamily rank for the monophyletic microsoroid ferns; and the following five main branches are given the tribe rank here: Thylacoptereae, Goniophlebidae, Lecanoptereae, Microsoreae, and Lepisoreae. These proposed tribes differ from their earlier definition (Hennipman et al., 1990), since not only morphology but also

molecular data have now been used. This framework reveals our current understanding about the relationships of the microsoroid ferns. The delimitation of the proposed tribes is almost identical with the clades used by Kreier et al. (2008) except for the tribe Lecanoptereae, which contains both Lecanopteroid and Membranaceoid clades (Kreier et al., 2008).

Tribe **Thylacoptereae** C.C. Chen & H. Schneider, **trib. nov.** —TYPE: *Thylacopteris* Kunze ex J. Smith

Only one genus *Thylacopteris* and one species *T. papillosa* was included in this study. *Thylacopteris* is a small genus with only two species. The distinguishing characters of this genus include free venation, the articulation of the lateral segments with the rachis, and jigsaw-puzzle-shaped rhizome scales with a warty inner thickened layer. (Rödl-Linder, 1994).

Tribe **Goniophlebidae** C.C. Chen & H. Schneider, **trib. nov.** —TYPE: *Goniophlebium* (Blume) C. Presl

This tribe contains only one genus, *Goniophlebium*, in a broad sense following the latest treatment (Kreier et al., 2008; PPG I, 2016). The distinguishing characters of *Goniophlebium* include simple-veined, longitudinal sclerenchyma strands in the rhizome and deltoid, pseudopeltate and clathrate rhizome scales (Rödl-Linder, 1990). However, some authors (Zhang et al., 2013) prefer to adopt concepts recognizing several smaller genera. These classifications recognize, besides *Goniophlebium* sensu stricto, the genera *Metapolypodium*, *Polypodiastrium*, and *Polypodiodes*. The type species of these small genera are in different well-supported subclades which indicates consistency between small genera classification and our inferred phylogenetic relationships (Fig. 1, Table 4). However, the current sampling of *Goniophlebium* is rather incomplete and a denser sampling is needed to address the arguments presented by Rödl-Linder (1990).

Tribe **Lecanoptereae** C.C. Chen & H. Schneider, **trib. nov.** —TYPE: *Lecanopteris* Reinw.

There are four clades in this group. In addition to the genus *Lecanopteris*, the three clades MG1, MG2, and MG3 contain species that were treated either as *Colysis* or *Microsorium* in the past. Of them, the MG1 clade contains two species in this study, *Asian Microsorium membranaceum* and *M. lastii* from Madagascar. In addition, a further putative member of this clade is arguably the Madagascan endemic *M. leandrianum* Tardieu (Kreier et al., 2008). These species within MG1 have unique plastid genome, biogeography, and morphological characters such as extremely thin

and membranaceous lamina, and have been named *Bosmania* Testo in the most recent study (Testo et al., 2019). The clades MG2 and MG3 consist of species mainly distributed in Oceania, especially Australia and New Zealand and *Lecanopteris* is mainly a southeast Asian and Malaysian genus with highly distinct morphological features (i.e. intercellular cavities in the rhizome) related to their relationships with ants (Haufler et al., 2003).

Our results show *Lecanopteris*, MG2, and MG3 as each being monophyletic and highly supported whether alone or together (Fig. 1). *Lecanopteris* and MG3 are monophyletic and sister of MG2. This structure is congruent with the previously results (Testo & Sundue, 2014; Nitta et al., 2018). However, another relationship with *Lecanopteris* and MG2 as sisters and together forming a sister clade of MG3 has been found (Schneider et al., 2006; Testo et al., 2019).

The delimitation and the possible new ranks of the three clades *Lecanopteris*, MG2 and MG3 are discussed here with three options. First, each of the three clades represents a different genus; this would keep the current definition and scope of *Lecanopteris* with another two generic names to stand for MG2 and MG3. Of them, the generic name *Dendroconche* Copel. will be applied for MG3 with the type *D. annabellae* (H.O. Forbes) Copel. (= *M. linguiforme*). This has been published recently (Testo et al., 2019), with the new generic name *Zealandia* Testo & A. R. Field also for MG2.

Second, extending the genus *Lecanopteris* to include also MG3 and another generic name for MG2 (*Zealandia*). Although clade MG3 does not have the apomorphic characters of the ant fern genus *Lecanopteris* (i.e. cavities in the rhizome), one of the species, *Microsorium linguiforme*, occasionally has internal rhizome cavities that might be interpreted as being homologous with the cavities found in *Lecanopteris* (Bosman, 1991; Haufler et al., 2003). In addition, the ants are observed living under the rhizomes of some plants of *Colysis ampla* (= *Dendroconche ampla*) (Testo et al., 2019). External ant housing is also found in *Lecanopteris mirabilis* which is a sister of the species of *Lecanopteris* with intrarhizome ant housing. Rhizome cavities have not been found in the any of the species comprising MG2 so far. Despite of this ambiguity, this option is less suitable because robust support for the clade is lacking as mentioned above; more samples and studies of morphological characters are still needed.

The last option is to extend *Lecanopteris* to include both MG2 and MG3 forming *Lecanopteris* sensu lato. The geographical range (Oceania for MG2 and MG3) and intercellular cavities (*Lecanopteris*) may roughly distinguish this clade from the other microsoroid ferns, but this large genus would still perhaps not be the best option because it would be morphologically poorly defined (Schneider et al., 2006; Testo et al., 2019).

Tribe **Microsoreae** V.N.Tu; Novosti Sist. Vyssh. Rast. 18: 18, 1981 —TYPE:

Microsorium Link

This tribe has also been found in previous studies containing the main clades of the core *Microsorium* species, although the subdivision of the tribe was not solved due to limited sampling and markers (Kreier et al., 2008; Nitta et al., 2018). In the present study we found four clades consisting of core *Microsorium*, MG4, *Leptochilus*, and MG5. Of them, the former two clades, and the latter two clades are sisters to each other (Fig. 1).

The core *Microsorium* clade contains two type species, *M. punctatum* and *M. scolopendria*, representing the genera *Microsorium* and *Phymatosorus*, respectively. Several authors have accepted *Phymatosorus* as a distinct genus based on the morphological characters such as anadromous tertiary vein and superficial or sunken sori (Hennipman et al., 1990; Bosman, 1991), but it is not a monophyletic group in our phylogenetic tree (Fig. 1). In addition to the type species in the core *Microsorium* clade, the species of *Microsorium* can be found also in another two clades, MG4, MG5 of Microsoreae. The generic name *Phymatosorus* could be applied for the branch with the type species but this would require several new generic names to be created. Besides, hybrids occur frequently between this and the species of its sister branch (Nitta et al., 2018). Therefore, it is better to merge *Phymatosorus* under the generic name *Microsorium*.

The clade *Leptochilus* includes many type species representing various genera that have previously been considered distinct, such as *Colysis*, *Kontumia*, *Kaulinia*, *Myuropteris*, *Nistarika*, and *Paraleptochilus* (Table 4). The species within this clade are morphologically diverse. *Leptochilus macrophyllus* appears to have diverged first followed by *L. pteropus* (widely known as *Microsorium pteropus*) and the rest of the species. Our results are congruent with those recently found by Zhang et al. (2019). The tribe Microsoreae is monophyletic but it would not be suitable to combine all four clades under one genus because of the large number and diversity of the species. Instead, suitable subdivisions would be needed. The species of *Leptochilus* are mostly terrestrial unlike those of *Microsorium* that are mostly epiphytes. This would lend support for maintaining its generic status. However, this would automatically create a paraphyletic *Microsorium* and thus new generic names would be needed for the clades MG4 and MG5. At this point no such names are proposed because we think that more detailed studies, including morphological characters, are needed to provide robust delimitation for these clades, and the core *Microsorium*.

Tribe **Lepisoraeae** Ching ex E Hennipman, P Veldhoen & KU Kramer; Fam. Gen. Vasc. Pl. I: 207, 1990 —TYPE: *Lepisorus* (J.Sm.) Ching

The tribe Lepisoreae contains seven well-supported clades, with each of them representing a genus recognized in PPG I (2016). *Paragramma* is the first clade and following two large clades which consist of the rest six genera. One of large clades is composed of five smaller genera: *Lemmaphyllum*, *Neolepisorus*, *Tricholepidium*, *Neocheiropteris*, and *Lepidomicrosorium*. The other main clade includes only one large and diverse genus, *Lepisorus*. Wang et al. (2010a) divided *Lepisorus* into nine subclades, which is congruent with our results (Fig. 2). The species *L. accedens* (= *Weatherbya accedens*) was recently supported as being embedded in the genus *Lepisorus* (Wei et al., 2017), and our results show it as sister to the subclade III but with weak support (Fig. 2; aLRT = 71.3% / aBayes = 0.75/ UFBoot = 98.0% / PP = 0.86).

Summary

Our efforts to infer a phylogeny of the microsoroid ferns, with sampling of over 70% of the species, provided support for the tribes as presented above. Of the five new groups of the microsoroid ferns that differ from the current genera of PPGI (2016), MG1-MG3 are recently provided the generic names *Bosmania*, *Zealandia*, and *Dendroconche*, respectively (Testo et al., 2019). However, MG4 and MG5, which have been included in the genera *Microsorium* and *Phymatosorus*, need further more detailed study including also morphological characters in order to provide a practical and useful classification. In addition to these two groups, the species delimitation such as for *Lepidomicrosorium superficiale* needs also further work. We found the markers *atpA* and *matK* to provide useful information for inferring phylogeny of the microsoroid ferns, but the number of sampled terminals for these two is still very limited. In addition, nuclear markers should be considered as well since they have revealed introgression or hybridization deeper in the tree (Nitta et al., 2018).

ACKNOWLEDGEMENTS

The authors acknowledge the financial support by the Chinese Academy of Sciences to HS. They also acknowledge the support by the molecular laboratory facilities team and fresh material assistance from XTBG. In addition, we appreciate colleagues Cheng-Wei Chen, Li-Yaung Kuo, Chun-Ming Chen, Daniele Cicuzza and Xianchun Zhang for providing important material.

REFERENCES

- Anisimova, M., Gil, M., Dufayard, J.F., Dessimoz, C., Gascuel, O., 2011. Survey of branch support methods demonstrates accuracy, power, and robustness of fast-likelihood-based approximation scheme. *Syst. Biol.* 60, 685-699.
<https://doi.org/10.1093/sysbio/syr041>.

- Bosman, M., 1991. A monograph of the fern genus *Microsorium* (Polypodiaceae), including an attempt towards a reconstruction of the phylogenetic history of the microsoroids. Leiden Bot. Ser. 14, 1–161.
- Brownsey, P.J., Perrie, L.R., 2014. Polypodiaceae (excluding Notogrammitis). In: Breitwieser, I., Heenan, P.B., Wilton, A.D. Flora of New Zealand - Ferns and Lycophytes. Fascicle 1. Manaaki Whenua Press, Lincoln.
- Edger, R.C., 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Res. 32, 1793-1797.
- Farris, J.S., Albert, V.A., Källersjö, M., Lipscomb, D., Kluge, A.G., 1996. Parsimony jackknifing outperforms neighbor-joining. Cladistics 12, 99-124.
- Fraser-Jenkins, C.R., 2008. Taxonomic revision of three hundred Indian subcontinental Pteridophytes: with a revised census list; a new picture of fern-taxonomy and nomenclature in the Indian subcontinent. Bishen Singh Mahendra Pal Singh.
- Goloboff, P.A., 1999. Analyzing large data sets in reasonable times: solutions for composite optima. Cladistics 15, 415-428.
- Goloboff, P. A., Farris, J. S., Nixon, K., 2008. TNT, a free program for phylogenetic analysis. Cladistics 24, 774-786.
- Goloboff, P. A., Catalano, S. A., 2016. TNT version 1.5, including a full implementation of phylogenetic morphometrics. Cladistics 32, 221-238.
- Guindon, S., Dufayard, J.F., Lefort, V., Anisimova, M., Hordijk, W., Gascuel, O., 2010. New algorithms and methods to estimate maximum-likelihood phylogenies: assessing the performance of PhyML 3.0 Syst. Biol. 5, 307-321. <https://doi.org/10.1093/sysbio/syq010>.
- Hall, T.A., 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucl. Acids. Symp. Ser. 41, 95-98.
- Hasebe, M., Omori, T., Nakazawa, M., Sano, T., Kato, M., Iwatsuki, K., 1994. rbcL gene sequences provide evidence for the evolutionary lineages of leptosporangiate ferns. Proc. Natl. Acad. Sci. U.S.A. 91, 5730-5734.
- Haufler, C.H., Grammer, W.A., Hennipman, E., Ranker, T.A., Smith, A.R., Schneider, H., 2003. Systematics of the ant-fern genus *Lecanopteris* (Polypodiaceae): testing phylogenetic hypotheses with DNA sequences. Syst. Bot. 28, 217-228.
- Hennipman, E., Veldhoen, P., Kramer, K.U., Price, M.G., 1990. Polypodiaceae, in: Kramer, K.U. and Green, P.S. (Eds), The families and genera of vascular plants. Vol. I. Pteridophytes and gymnosperms. Springer-Verlag, Berlin. Pp.203-230.
- Hettterscheid, W.L.A., Hennipman, E., 1984. Venation patterns, soral characteristics, and shape of the fronds of the microsoroid Polypodiaceae. Meded. bot. Mus. Herb. Rijksuniv. Utrecht. 540, 11-47.
- Holttum, R.E., 1966. New ferns from Malesia. Kew Bull. 20, 455-460.
- Kalyaanamoorthy, S., Minh, B.Q., Wong, T.K., von Haeseler, A., Jermin, L.S., 2017. ModelFinder: fast model selection for accurate phylogenetic estimates. Nat. Methods 14, 587-589. <https://doi.org/10.1038/nmeth.4285>.
- Kaulfuss, G.F., 1824. Enumeratio filicum quas in itinere circa terram legit Cl. Adalbertus de Chamisso adiectis in omnia harum plantarum genera permultasque species non satis cognitatas vel novas animadversionibus. Sumtibus Caroli Cnobloch, Leipzig.
- Kim, C., Zha, H.G., Deng, T., Sun, H., Wu, S.G., 2013. Phylogenetic position of *Kontumia* (Polypodiaceae) inferred from four chloroplast DNA regions. J. Syst. Evol. 51, 154-163.
- Kreier, H.P., Zhang, X.C., Muth, H., Schneider, H., 2008. The microsoroid ferns: Inferring the relationships of a highly diverse lineage of Paleotropical epiphytic

- ferns (Polypodiaceae, Polypodiopsida). *Molec. Phylogenet. Evol.* 48, 1155-1167.
- Kuo, L.Y., Li, F.W., Chiou, W.L., Wang, C.N., 2011. First insights into fern matK phylogeny. *Molec. Phylogenet. Evol.* 59, 556-566.
- Lanfear, R., Frandsen, P.B., Wright, A.M., Senfeld, T., Calcott, B., 2016. PartitionFinder 2: new methods for selecting partitioned models of evolution formolecular and morphological phylogenetic analyses. *Molec. Biol. Evol.* 34(3), 772-773. <https://doi.org/10.1093/molbev/msw260>.
- Lehtonen, S., 2011. Towards resolving the complete fern tree of life. *PLoS One* 6, e24851. <https://doi.org/10.1371/journal.pone.0024851>.
- Li, C., Lu, S., Yang, Q., 2004. Asian origin for *Polystichum* (Dryopteridaceae) based on rbcL sequences. *Chin. Sci. Bull.* 49, 1146-1150.
- Link H.F., 1833. *Hortus regius botanicus berolinensis descriptus*, Berolini.
- Maddison, W.P., Maddison, D.R., 2017. Mesquite: a modular system for evolutionary analysis. Version 3.31. <http://mesquiteproject.org>.
- Minh, B.Q., Guyen, M.A.T., von Haessler, A., 2013. Ultrafast approximation for phylogenetic bootstrap. *Molec. Biol. Evol.* 30, 1188-1195. <https://doi.org/10.1093/molbev/mst024>.
- Nayar, B.K., 1964. *Kaulinia*, a new genus of Polypodiaceous ferns. *Taxon* 13: 67-69.
- Nguyen, L.T., Schmidt, H.A., von Haeseler, A., Minh, B.Q., 2014. IQ-Tree: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molec. Biol. Evol.* 32, 268-274. <https://doi.org/10.1093/molbev/msu300>.
- Nitta, J.H., Amer, S., Davis, C.C., 2018. *Microsorium* × *tohieaense* (Polypodiaceae), a New Hybrid Fern from French Polynesia, with Implications for the Taxonomy of *Microsorium*. *Syst. Bot.* 43, 397-413.
- Nixon, K.C., 2002. Winclada, Version 1.00.08. Software published by the author, Ithaca, NY. Available on-line @ www.diversityoflife.org/winclada/.
- Nixon, K.C., Davis, J.I., 1991. Polymorphic taxa, missing values and cladistic analysis. *Cladistics* 7, 233-241.
- Nooteboom, H.P., 1997. The microsorioid ferns (Polypodiaceae). *Blumea* 42, 261-395.
- Pichi Sermolli, R.E.G., 1973. *Fragmenta pteridologiae* (IV). *Webbia* 28, 445-477.
- Platnick, N.I., Griswold, C.E., Coddington, J.A., 1991. On missing entries in cladistic analysis. *Cladistics* 7, 337-343.
- PPG I, 2016. A community-derived classification for extant lycophytes and ferns. *J. Syst. Evol.* 54, 563-603. <https://doi.org/10.1111/jse.12229>.
- Rambaut, A., Drummond, A.J., 2007. Tracer v.1.4. Available from <http://beast.bio.ed.ac.uk/Tracer>.
- Rödl-Linder, G., 1990. A monograph of the fern genus *Goniophlebium*. *Blumea* 34, 277-423.
- Rödl-Linder, G., 1994. A monograph of the fern genus *Thylacopteris* (Polypodiaceae). *Blumea* 39: 351-364.
- Ronquist, F., Huelsenbeck, J.P., 2003. MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19, 1572-1574.
- Schneider, H., Ranker, T.A., Russell, S.J., Cranfill, R., Geiger, J.M.O., Agurauja, R., Wood, K.R., Grundmann, M., Klobardanz, K., Vogel, J.C., 2005. Origin of the endemic fern genus *Diellia* coincides with the renewal of Hawaiian terrestrial life in the Miocene. *Proc. R. Soc. Lond., B, Biol. Sci.* 272(1561), 455-460.
- Schneider, H., Kreier, H.P., Perrie, L.R., Brownsey, P.J., 2006. The relationships of *Microsorium* (Polypodiaceae) species occurring in New Zealand. *N.Z. J. Bot.* 44,

121-127.

- Schneider, H., Janssen, T., Hovenkamp, P., Smith, A.R., Cranfill, R., Haufler, C.H., Ranker, T.A., 2004a. Phylogenetic relationships of the enigmatic Malesian fern *Thylacopteris* (Polypodiaceae, Polypodiidae). *Int. J. Plant Sci.* 165, 1077-1087.
- Schneider, H., Smith, A.R., Cranfill, R., Hildebrand, T.J., Haufler, C.H., Ranker, T.A., 2004b. Unraveling the phylogeny of polygrammoid ferns (Polypodiaceae and Grammitidaceae): exploring aspects of the diversification of epiphytic plants. *Molec. Phylogenet. Evol.* 31, 1041-1063.
- Schuettpelz, E., Korall, P., Pryer, K.M., 2006. Plastid atpA data provide improved support for deep relationships among ferns. *Taxon* 55, 897-906.
- Schuettpelz, E., Pryer, K.M., 2007. Fern phylogeny inferred from 400 leptosporangiate species and three plastid genes. *Taxon* 56, 1037-1037.
- Small, R.L., Lickey, E.B., Shaw, J., Hauk, W.D., 2005. Amplification of noncoding chloroplast DNA for phylogenetic studies in lycophytes and monilophytes with a comparative example of relative phylogenetic utility from Ophioglossaceae. *Molec. Phylogenet. Evol.* 36, 509-522.
- Smith, A.R., Pryer, K.M., Schuettpelz, E., Korall, P., Schneider, H., Wolf, P.G., 2006. A classification for extant ferns. *Taxon* 55, 705-731.
- Taberlet, P., Gielly, L., Pautou, G., Bouvet, J., 1991. Universal primers for amplification of three non-coding regions of chloroplast DNA. *Plant Mol. Biol.* 17, 1105-1109.
- Testo, W.L., Field, A.R., Sessa, E.B., Sundue, M., 2019. Phylogenetic and Morphological Analyses Support the Resurrection of *Dendroconche* and the Recognition of Two New Genera in Polypodiaceae Subfamily Microsoroideae. *Systematic Botany* 44, 1-16.
- Trewick S.A., Morgan-Richards, M., Russell, S.J., Henderson, S., Rumsey, F.J., Pínter, I., Barrett, J.A., Gibby, M., Vogel, J.C., 2002. Polyploidy, phylogeography and Pleistocene refugia of the rockfern *Asplenium ceterach*: evidence from chloroplast DNA. *Mol. Ecol.* 11, 2003-2012.
- Trifinopoulos, J., Nguyen, L.T., von Haesler, A., Minh, B.Q., 2016. W-IQ-Tree: a fast online phylogenetic tool for maximum likelihood analysis. *Nucleic Acid Res.* 44, W232-W235. <https://doi.org/10.1093/nar/gkw256>.
- Wang, L., Qi, X.P., Xiang, Q.P., Heinrichs, J., Schneider, H., Zhang, X.C., 2010a. Phylogeny of the paleotropical fern genus *Lepisorus* (Polypodiaceae, Polypodiopsida) inferred from four chloroplast DNA regions. *Molec. Phylogenet. Evol.* 54, 211-225.
- Wang, L., Schneider, H., Zhang, X.C., Xiang, Q.P., 2012. The rise of the Himalaya enforced the diversification of SE Asian ferns by altering the monsoon regimes. *BMC Plant Biol.* 12, 210.
- Wang, L., Wu, Z.Q., Xiang, Q.P., Heinrichs, J., Schneider, H., Zhang, X.C., 2010b. A molecular phylogeny and a revised classification of tribe Lepisoreae (Polypodiaceae) based on an analysis of four plastid DNA regions. *Bot. J. Linn. Soc.* 162, 28-38.
- Wang, L., Wu, Z.Q., Bystriakova, N., Ansell, S.W., Xiang, Q.P., Heinrichs, J., Schneider H., Zhang, X.C., 2011. Phylogeography of the Sino-Himalayan fern *Lepisorus clathratus* on “the roof of the world”. *PLoS One* 6(9), e25896. <https://doi.org/10.1371/journal.pone.0025896>.
- Wei, X.P., Wei, R., Zhao, C.F., Zhang, H.R., Zhang, X.C., 2017. Phylogenetic Position of the Enigmatic Fern Genus *Weatherbya* (Polypodiaceae) Revisited: Evidence from Chloroplast and Nuclear Gene Regions and Morphological Data. *Int.*

- J. Plant Sci. 178, 450-464.
- Wheeler, W.C., 2012. Systematics: a course of lectures. John Wiley & Sons.
- Wheeler, W.C. et al., 2017. The spider tree of life: phylogeny of Araneae based on target-gene analyses from an extensive taxon sampling. *Cladistics* 33, 574-616.
- Wolsan, M., Sato, J.J., 2010. Effects of data incompleteness on the relative performance of parsimony and Bayesian approaches in a supermatrix phylogenetic reconstruction of Mustelidae and Procyonidae (Carnivora). *Cladistics* 26, 168-194.
- Wu, S.G., Pan, K.L., Xiang, J.Y., 2005. A new genus and two new species of ferns from Vietnam. *Novon* 15: 245-249.
- Zhang, L., Lu, N.T., Zhou, X.M., Chen, D.K., Knapp, R., Zhou, L., Guo, L., Luong, T.T., Sun, H., Gao, X.F., Zhang, L. B. (2019). A plastid phylogeny of the Old World fern genus *Leptochilus* (Polypodiaceae): Implications for cryptic speciation and progressive colonization from lower to higher latitudes. *Molec. Phylogenet. Evol.* 134, 311-322.
- Zhang, X.C., Lu, S.G., Lin, Y.X., Qi, X.P., Moore, S.J., Xing, F.W., Wang, F.G., Hovenkamp, P.H., Gilbert, M.G., Nooteboom, H.P., Parris, B.S., Haufler, C.H., Kato, M., Smith, A.R., 2013. Polypodiaceae. In: Wu, Z.Y., Raven, P.H., Hong, D.Y. (Eds.) *Flora of China*. Vol. 2–3. Beijing: Science Press and St. Louis: Missouri Botanical Garden Press, pp. 758–850.

Color should be used only for Figure 4 in print.

Table 1 Summary of sampled specimens. Specimen information is organized as follows: locality or cultivated, collector or specimen number, and herbaria abbreviations which are given in parenthesis following the Index Herbariorum. GenBank Accession Numbers for six plastid regions: *rbcL*, *rps4* & *rps4-trnS*, *trnL* & *trnL-trnF*, *atpA*, *atpB* & *rbcL-atpB*, *matK*. The dash indicates missing sequence. Sequences IN BOLD are novel; marked with ** were downloaded from Genbank as complete genome, which were used to extract data of each regions used in this study.

Table 2 List of primers for amplifying the gene regions used in this study.

Table 3 Information of alignment dataset, best-fitting models and parameter values of large and small dataset for separate genes of *rbcL*, *rps4* & *rps4-trnS* IGS, *trnL-trnF* region, *atpA*, *atpB* & *rbcL-atpB* IGS, and *matK*.

Table 4 The proposed generic names, following the status of the name which based on the Tropicos database (<https://www.tropicos.org/>), type species & if it included in this study. Group indicates the clade that the type species of the genus belongs to; Mono indicates if the genus is monophyletic or not, and mark * means only one species in this study; the last column shows original and lectotype publications. Names in bold used in this study. Abbreviation: leg., legitimate; nom. cons., conserved name; nom. rej., name rejected; illeg. hom., name illegitimated due to homonymy; LT, lectotype; -, lack of data.

Table 5 List of generic name and grouping of the microsoroid ferns in selected taxonomic and phylogenetic works. Abbreviations: GO, goniophleboid clade; LC, lecanopteroid clade; LP, leporoid clade; ME, membranaceoid clade; MI, microsoroid s.s. clade; TH, thylacopteroid clade; Sf.LO, Subfamily Loxogrammoideae; Sf.DN, Subfamily Drynarioideae; Sf.MI, Subfamily Microsoroideae; T.PO, Tribe Polypodiaceae; T.LP, Tribe Lepisoreae; T.MI, Tribe Microsoreae; T.GO, Goniophlebieae; T.TH, Thylacoptereae; T.LC, Lecanoptereae.

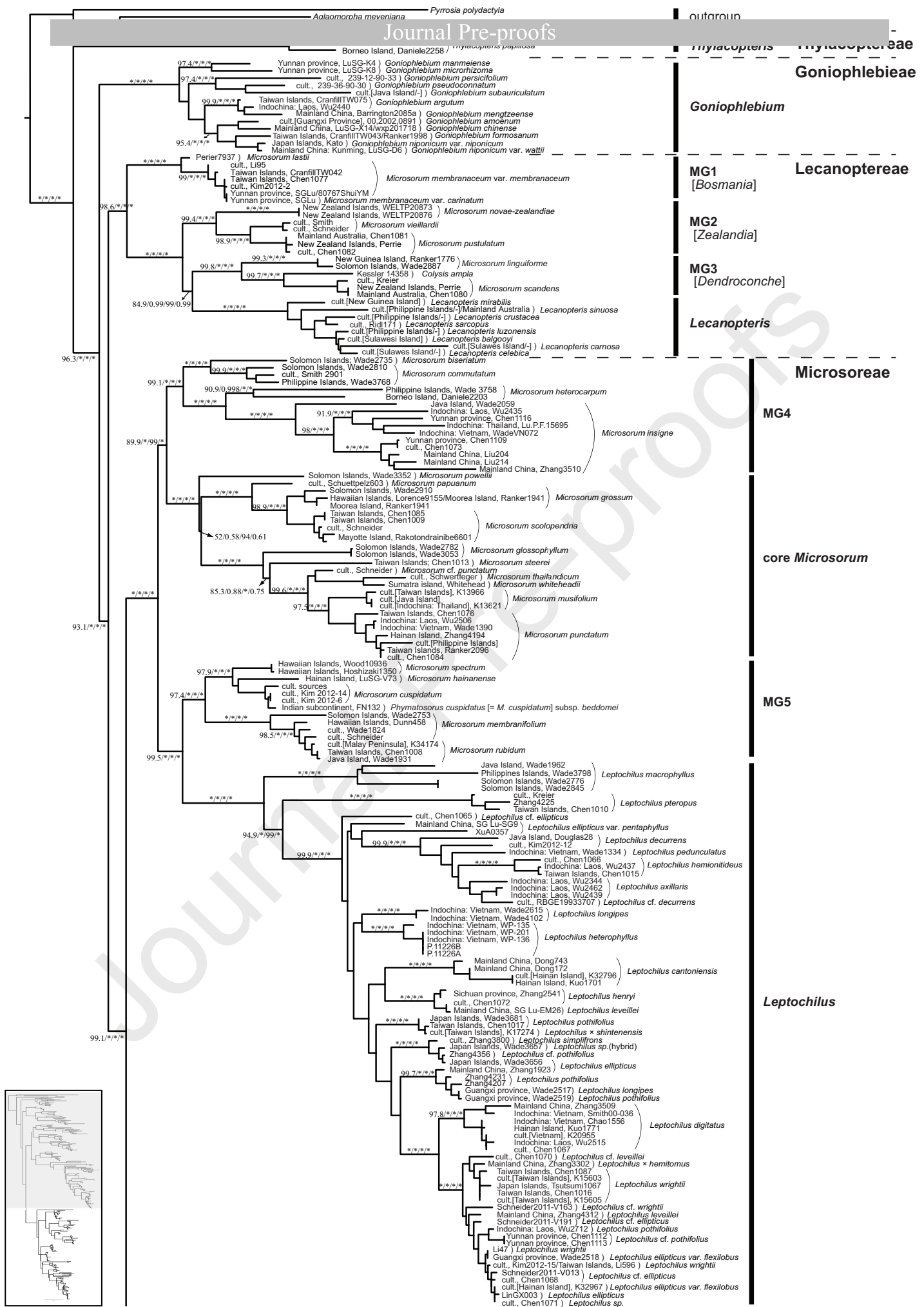
Fig. 1 Phylogenetic hypothesis depicting the phylogenetic relationships of the tribes Thylacopterae, Goniophlebidae, Lecanopterae, and Microsoreae. The generic names with square brackets indicate the latest results (Testo et al., 2019) that are not included in PPG I (2016). Branch lengths correspond to the estimated number of substitution events. The values are for the Shimodaira-Hasegawa-like approximate likelihood ratio test (SH-aLRT, %), p-values of the Bayesian-like transformation of aLRT statistics (abayes), ultrafast bootstrap analysis (UFBoot, %), and posterior confidence values of BI (pp) respectively. The asterisk, *, indicates branches with maximum values of the indices used.

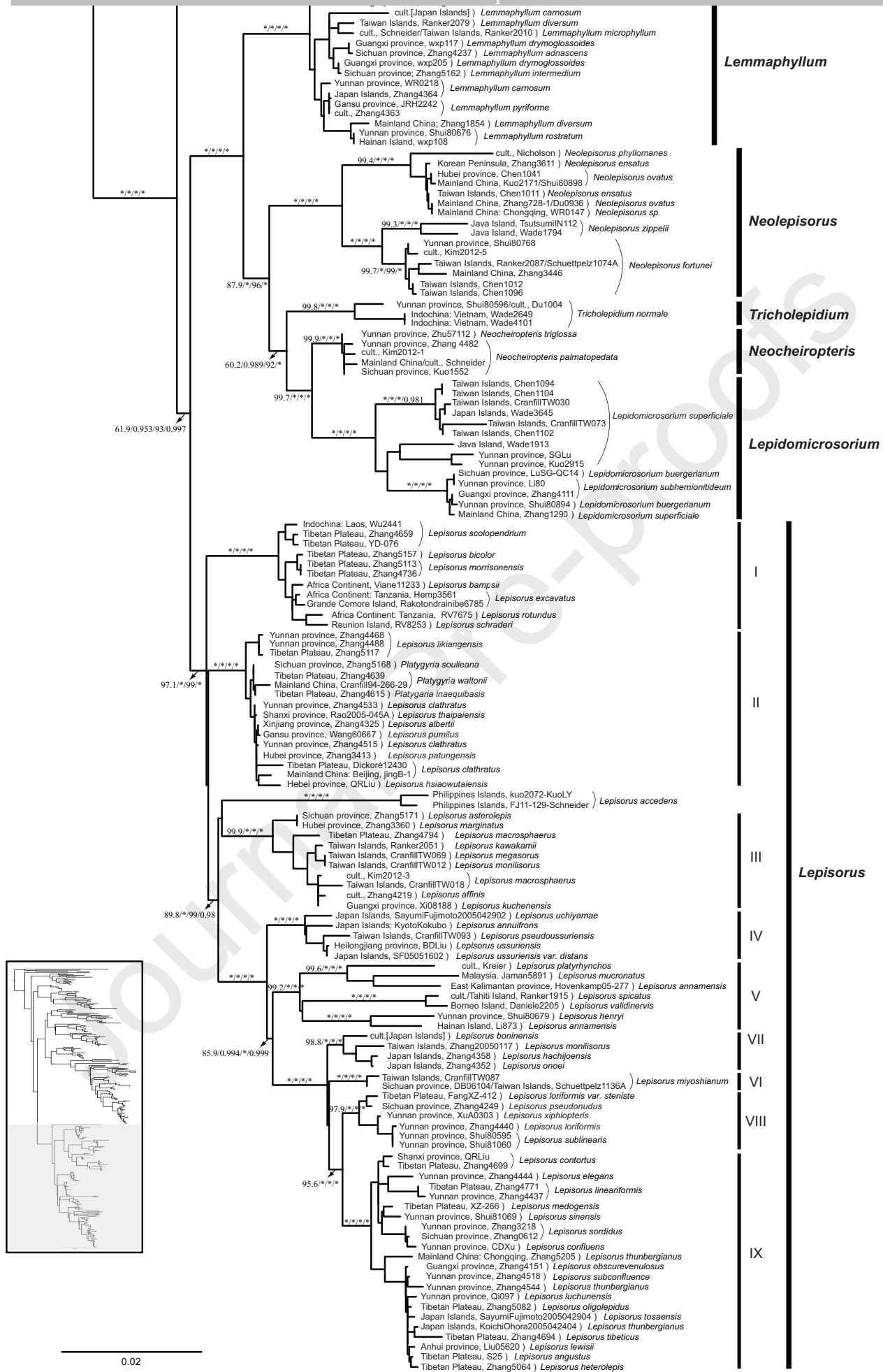
Fig. 2 Phylogenetic hypothesis depicting the phylogenetic relationships of the tribe Lepisoreae, branch lengths correspond to the estimated number of substitution events. Subgroups from I to IX are based on the results of Wang et al. (2010b). The values as in Fig. 1. with the asterisk, *, indicating branches with maximum values of the indices.

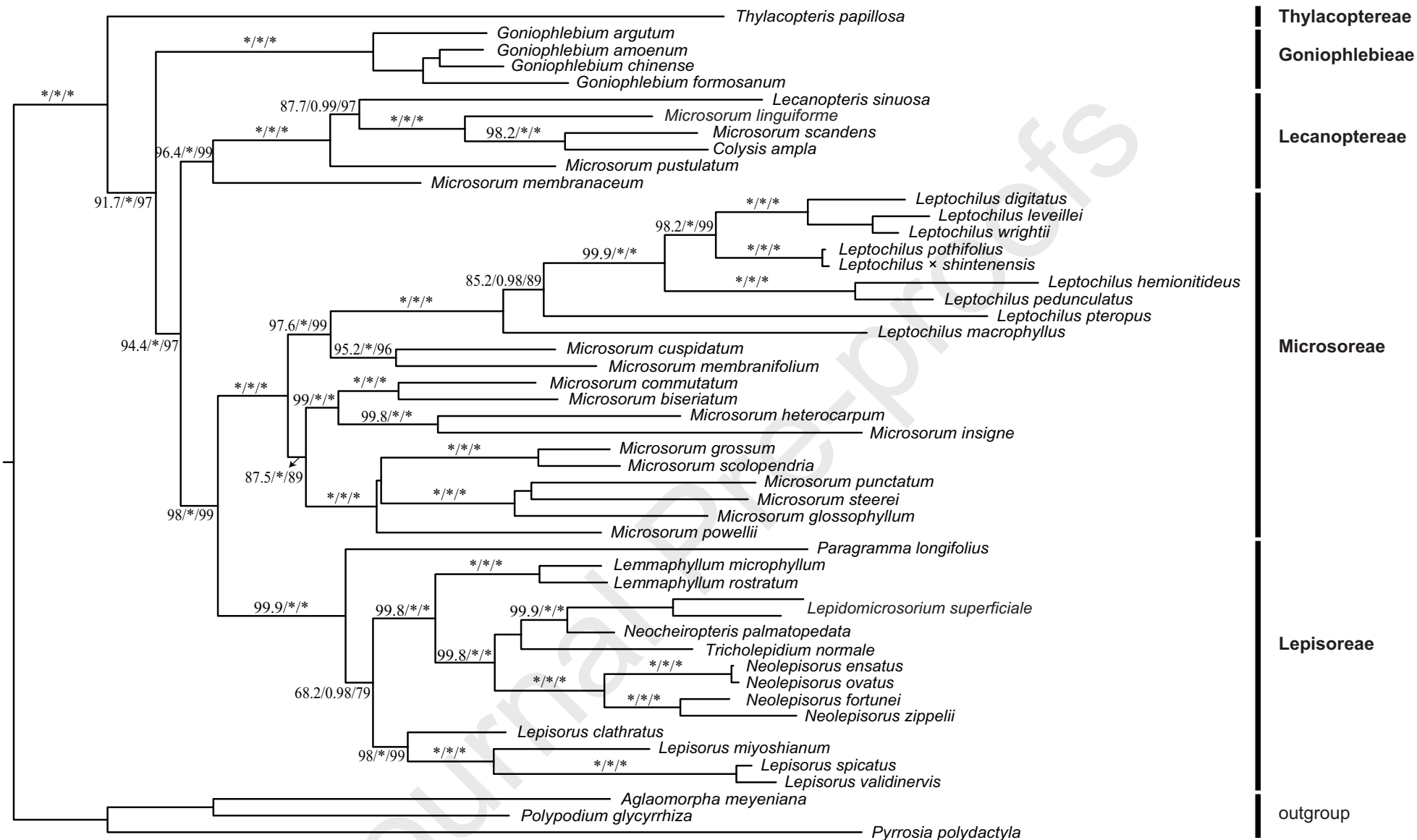
Fig. 3 Phylogenetic hypothesis depicting the phylogenetic relationships of the microsoroid ferns in small dataset, branch length correspond to the estimated number of substitution events. The values as in Fig. 1. with the asterisk, *, indicating branches with maximum values of the indices.

Fig. 4 Phylogenetic hypothesis depicting the phylogenetic relationships based on three large datasets. Three of the main groups or genera: core *Microsorium*, *Lepisorus*, and *Lepidomicrosorium* are showed also partly with their subclades indicated with purple, blue, and yellow colors. In addition, genus *Paragramma* is highlighted in red. The small squares above the branches indicate different values of Shimodaira-Hasegawa-like approximate likelihood ratio test (SH-aLRT), p-values of the Bayesian-like transformation of aLRT statistics (abayes), and ultrafast bootstrap analysis (UFBoot), respectively. The black color indicates values=1.00 (100%) in all tests; the gray color indicates the values <1.00 (100%) and >= 0.95 (95%) in abayes and UFBoot, whereas <100% and >= 80% in SH-aLRT; and white the values <0.95 (95%) in abayes and UFBoot, whereas < 80% in SH-aLRT. Geographical abbreviations: TW, Taiwan; JP, Japan; and YN, Yunnan (China).

Fig. 5 Consensus of 1714 equally parsimonious trees with a length of 7677 steps from the maximum parsimony analysis based on the large dataset (combining six gene regions). Subgroups from I to IX are based on the results of Wang et al. (2010b). The genera with square brackets are based on the results of Testo et al. (2019).

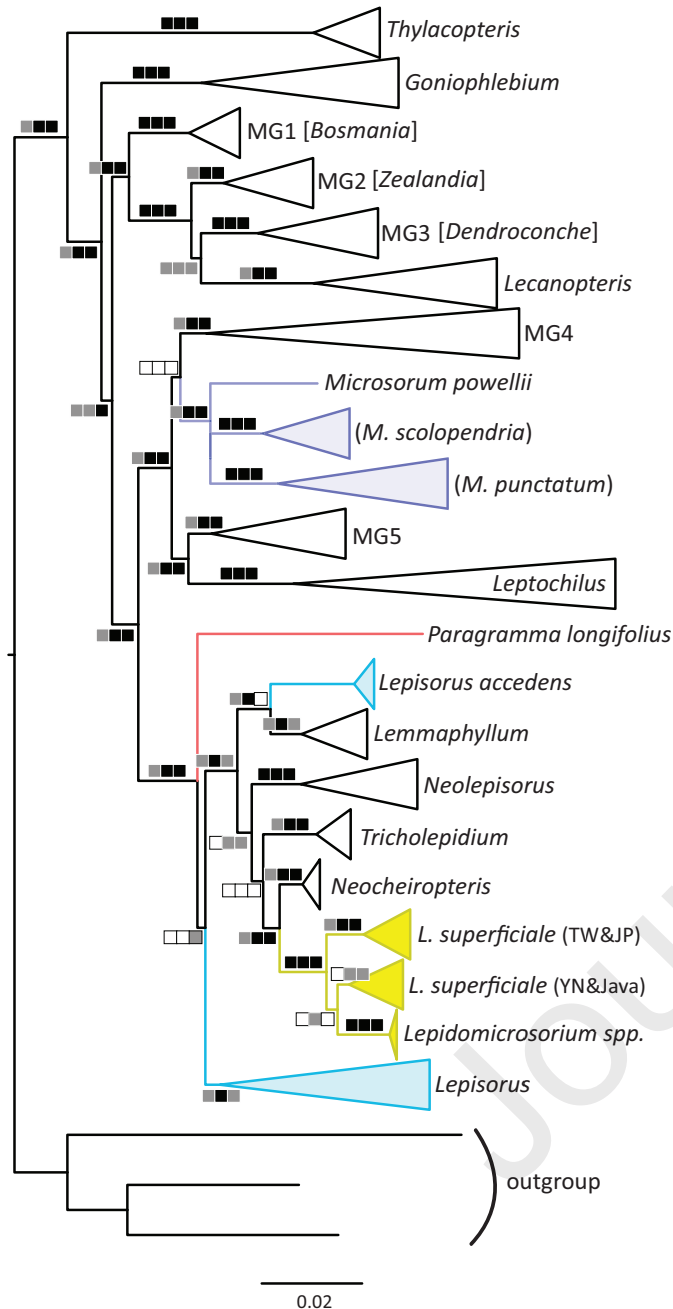






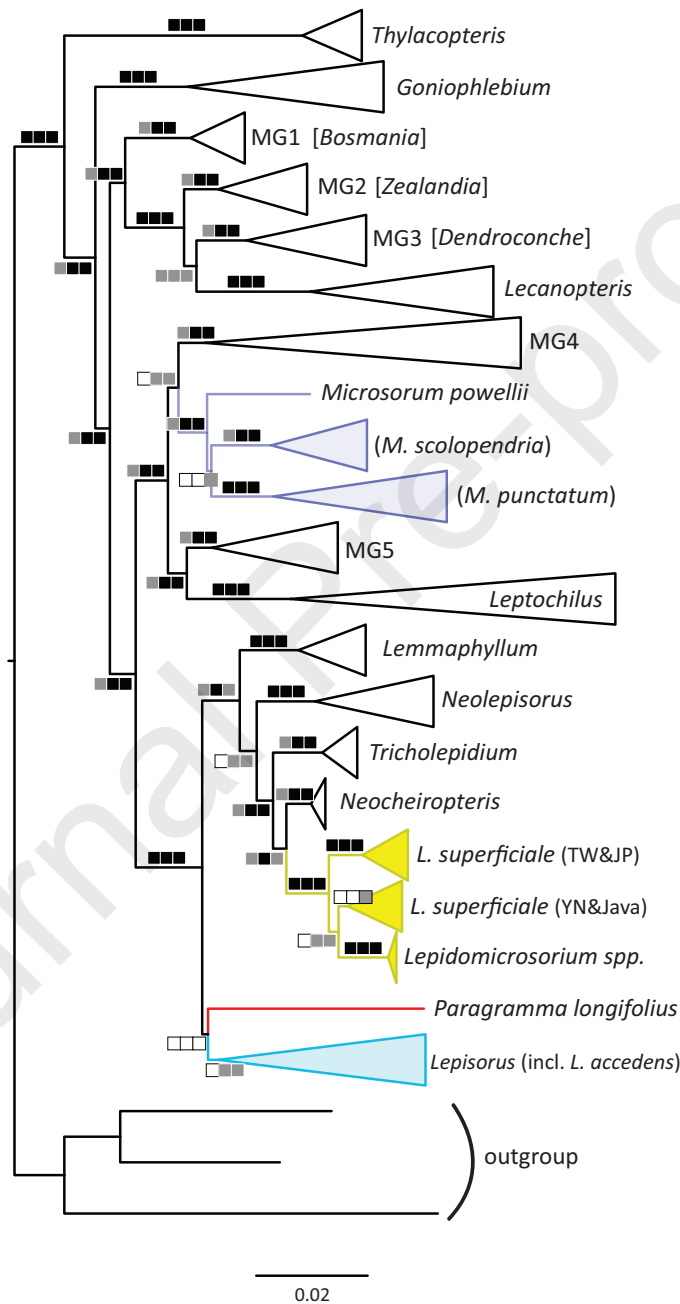
three-combination

(*rbcl*, *rps4* + *rps4-trnS*, *trnL+trnL-trnF*)



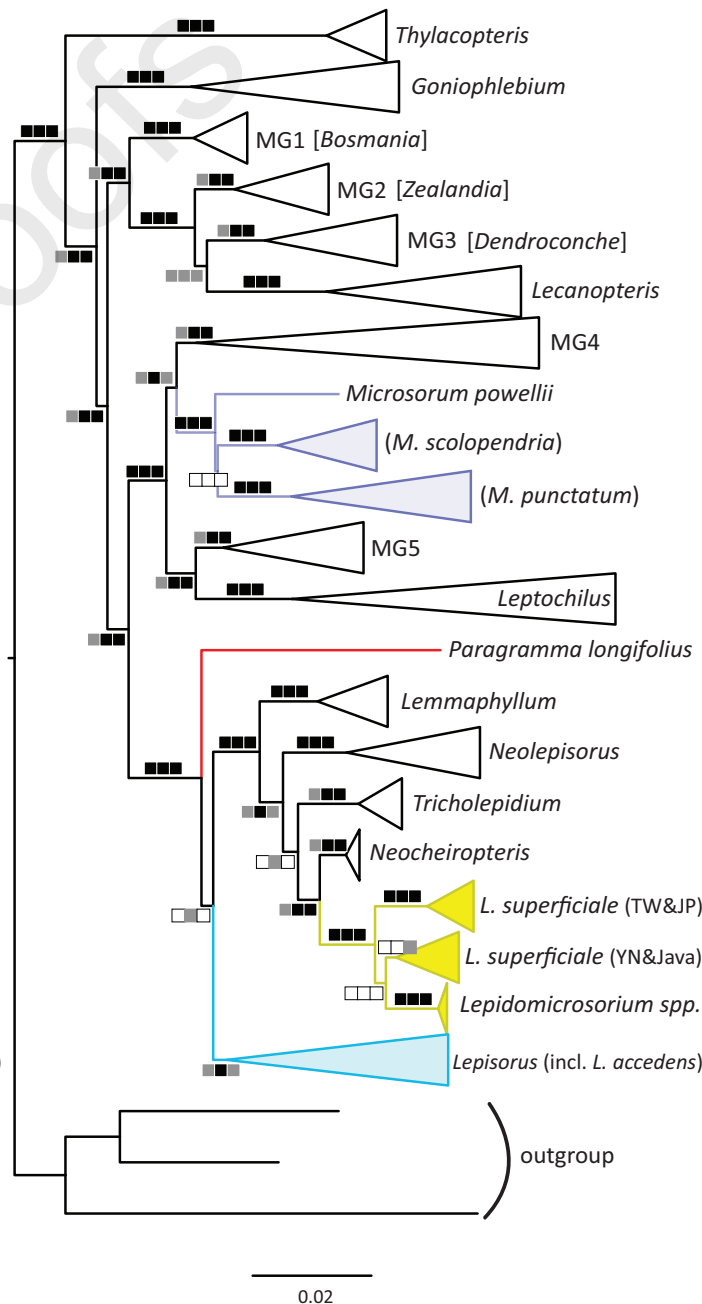
four-combination

(*rbcl*, *rps4* + *rps4-trnS*, *trnL+trnL-trnF*, *rbcl-atpB* + *atpB*)



six-combination

(*rbcl*, *rps4* + *rps4-trnS*, *trnL+trnL-trnF*, *rbcl-atpB* + *atpB*, *atpA*, *matK*)



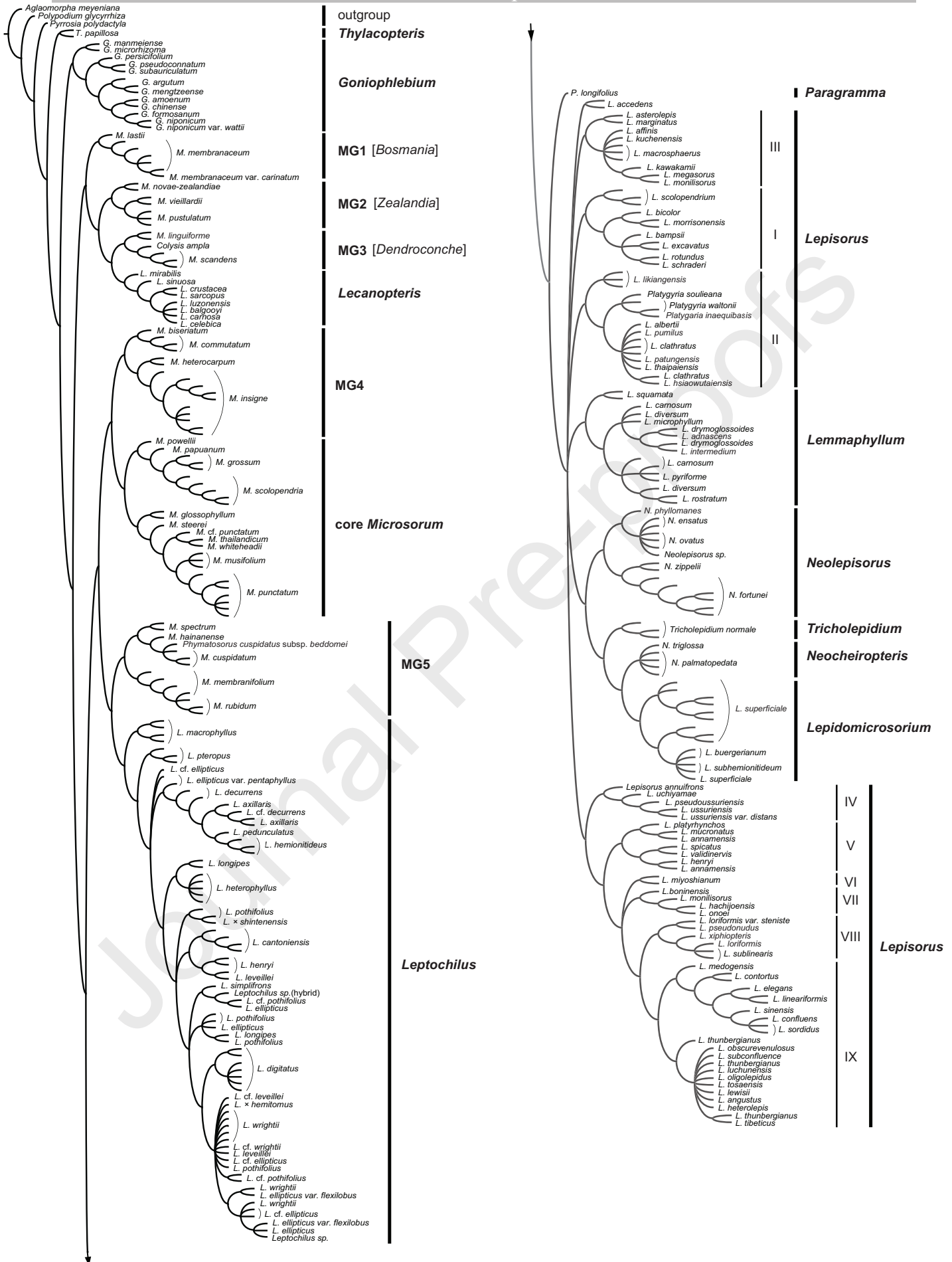


Table 1 Summary of sampled specimen. Specimen information is organized as follows: locality, collector or specimen number (deposited herbarium). GenBank Accession Numbers for six plastid regions: rbcL, rps4 & rps4-trnS, trnL & trnL-trnF, atpA, atpB & rbcL-atpB, matK. A dash indicates missing sequence. Sequences IN BOLD are novel; marked with * were downloaded from Genbank as complete genome, which were used to extract data of each regions used in this study.

Abbreviations: BGB, Botanical Garden Berlin-Dahlem; BGG, Old Botanical Garden Göttingen; BGH, Botanical Garden of the University of Heidelberg; BGM, Botanical Garden Munich-Nymphenburg; BGZ, Botanical Garden Zurich; CAG, Garden of Charles Alford; CBG, Cibodas Botanical Garden; DBG, Duke Botanical Garden; JNU, Jinan University; KBCC, Dr. Cecilia Koo Botanic Conservation Center; KBG, Kunming Botanical Garden; LBG, Leiden Botanical Garden; PE, Chinese National Herbarium; RBGE, Royal Botanic Garden Edinburgh; RBGK, Royal Botanic Gardens Kew; RBGV, Royal Botanic Gardens Victoria; SZBG, Fairylake Botanical Garden; TBG, Tuebingen Botanic Garden; UBDH, Universiti Brunei Darussalam; UBG,

Taxon name	Voucher of Accession	rbcL	rps4 & rps4-trnS	trnL & trnL-trnF	atpA	atpB & rbcL-atpB	matK
<i>Colysis amplia</i> Copel.	Kessler 14358 (VT)	KF570108	KF570109	KF570110	-	-	-
<i>Goniophlebium amoenum</i> (Wall. ex Mett.) Bedd.	cult. XTBG [Guangxi Province]; 00,2002,0891	MH665028	MH665091	MH665158	MH664988	MH665004	MH665018
<i>Goniophlebium argutum</i> (Wall. ex Hook.) J. Sm. ex Hook.	Taiwan Islands; Cranfill TW075 (UC)	DQ164442	DQ164473	DQ164505	-	-	-
<i>Goniophlebium argutum</i> (Wall. ex Hook.) J. Sm. ex Hook.	Indochina: Laos; Wu 2440 (KUN)	JX103709	JX103751	JX103793	-	JX103667	-
<i>Goniophlebium chinense</i> (Christ) X.C. Zhang	Mainland China: Chongqing; Lu SG-X14 (PYU)	DQ078630	DQ078637	-	-	-	-
	Mainland China; Wei X.P. wxp201718 (IMD)	-	-	-	-	-	MF450478
<i>Goniophlebium formosanum</i> (Baker) Rodl-Linder	Taiwan Islands; Cranfill TW043 (UC)	-	AY096224	DQ642235	-	-	-
	Taiwan Islands; Ranker 1998 (COLO)	-	-	-	EF463813	EF463495	-
<i>Goniophlebium manniense</i> (Christ) Rodl-Linder	Mainland China: Yunnan province; Lu SG-K4 (PYU)	DQ078628	DQ078631	-	-	-	-
<i>Goniophlebium mengtzeense</i> (Christ) Rodl-Linder	Mainland China; Barrington 2085a (UVM)	AY362560	AY362627	-	-	-	-
<i>Goniophlebium microrrhizoma</i> (C.B. Clarke ex Baker) Bedd.	Mainland China: Yunnan; Lu SG-K8 (PYU)	DQ078627	DQ078632	-	-	-	-
<i>Goniophlebium niponicum</i> (Mett.) Bedd. var. <i>niponicum</i>	Japan Islands; Kato et al. (TI)	-	AY362626	EU483027	-	-	-
<i>Goniophlebium niponicum</i> var. <i>wattii</i> (Bedd.) Bedd.	Mainland China: Kunming; Lu SG-D6 (PYU)	DQ078625	DQ078636	-	-	-	-
<i>Goniophlebium persicifolium</i> (Desv.) Bedd.	cult. BGB; 239-12-90-33 (B)	EU482933	EU482978	EU483028	-	-	-
<i>Goniophlebium pseudocannatum</i> (Copel.) Copel.	cult. BGB; 239-36-90-30 (B)	EU482934	EU482979	EU483029	-	-	-
<i>Goniophlebium subauriculatum</i> (Blume) C.Presl	cult. UCBG [Indonesia Islands: Java, (UC)]	AF470342	-	AY083645	-	-	-
	cult. BGG, Kreier s.n. (GOET)	-	DQ168812	-	-	-	-
<i>Lecanopteris balgooyi</i> Hennisman	cult. UBG [Sulawesi Island; David Klein s.n. (L)]	AF470328	-	AY083631	-	-	-
	Sulawesi Island; Hennisman s.n. (L)	-	EU482980	-	-	-	-
<i>Lecanopteris carnosia</i> (Reinw.) Blume	cult. UBG [Sulawesi Island; David Klein s.n. (L)]	AF470322	-	AY083625	-	-	-
	cult. RBGK; Cranfill 153 (UC)	-	AY096227	-	-	-	-
<i>Lecanopteris celebica</i> Hennisman	cult. UBG 85GR00170 [Sulawesi Island; Hennisman s.n. (L)]	AF470323	-	AY083626	-	-	-
	cult. BGG; Schneider s.n. (GOET)	-	EU482981	-	-	-	-
<i>Lecanopteris crustacea</i> Copel.	cult. UBG 82GR00292 [Philippine Islands; Franken and Roos 341(L)]	AF470329	-	AY083632	-	-	-
	cult. CAG; A.R. Smith (UC)	-	EU482982	-	-	-	-
<i>Lecanopteris luzonensis</i> Hennisman	cult. UBG [Philippine Islands; Hennisman 7820 (U, L)]	AF470325	-	AY083628	-	-	-
	cult. BGG; Schneider s.n. (GOET)	-	EU482983	-	-	-	-
<i>Lecanopteris mirabilis</i> (C. Chr.) Copel.	cult. UBG 665 [New Guinea Island; Hennisman s.n. (U)]	AF470330	EU482984	AY083633	-	-	-
<i>Lecanopteris sarcopus</i> (Teijsm. & Binn.) Copel.	cult. RBGE; Ridl 171 (E)	EU482935	EU482985	EU483030	-	-	-
<i>Lecanopteris sinuosa</i> (Hook.) Copel.	cult. UBG 87GR00087 [Philippine Islands; Hennisman 7821 (U, L)]	AF470321	-	AY083624	-	-	-
	cult. RBGK	-	AY362634	-	-	-	-
	Mainland Australia; Sankowsky 4169 (NSW)	-	-	-	KP164484	KP164491	-
<i>Lemmaphyllum adnascens</i> Ching	Mainland China: Sichuan province; Zhang 4237 (PE)	GU126694	GU126713	GU126724	-	GU126702	-
<i>Lemmaphyllum carnosum</i> (Wall. ex J. Sm.) C. Presl	cult. UCBG 50.0326 [Japan Islands; (UC)]	AF470332	AY362631	AY083635	-	-	-
<i>Lemmaphyllum carnosum</i> (Wall. ex J. Sm.) C. Presl	Mainland China: Yunnan province; Wei R et al. WR0218 (PE)	KX891370	KX891402	KX891355	-	KX891384	-
<i>Lemmaphyllum carnosum</i> (Wall. ex J. Sm.) C. Presl	Japan Islands; Zhang 4364 (PE)	GU126698	GU126717	GU126728	-	GU126706	-
<i>Lemmaphyllum drymoglossoides</i> (Baker) Ching	Mainland China: Guangxi province; Wei XP et al. wxp117 (PE)	KX891372	KX891403	KX891357	-	KX891385	-
<i>Lemmaphyllum drymoglossoides</i> (Baker) Ching	Mainland China: Guangxi province; Wu L et al. wxp205 (PE)	KX891373	KX891404	KX891358	-	KX891386	-
<i>Lemmaphyllum diversum</i> (Rosenst.) Tagawa	Taiwan Islands; Ranker 2079 (COLO)	EU482937	EU482987	EU483032	-	GU126707	-
<i>Lemmaphyllum diversum</i> (Rosenst.) Tagawa	Mainland China; Zhang 1854 (PE)	EU482939	EU482989	EU483034	-	-	-
<i>Lemmaphyllum intermedium</i> (Ching) Li Wang	Mainland China: Sichuan province; Zhang 5162 (PE)	GU126696	GU126715	GU126726	-	-	-
<i>Lemmaphyllum microphyllum</i> C. Presl	cult. BGG; Schneider s.n. (GOET)	EU482938	EU482988	EU483033	-	-	-
	Taiwan Islands; Ranker 2010 (COLO)	-	-	-	EF463824	EF463496	-
<i>Lemmaphyllum pyriforme</i> (Ching) Ching	Mainland China: Gansu province; Jiang RH JRH2242 (PE)	KX891374	KX891406	KX891361	-	KX891388	-

<i>Lemmaphyllum pyriforme</i> (Ching) Ching	cult. TBG; Zhang 4363 (PE)	GU126695	GU126714	GU126725	-	GU126703	-
<i>Lemmaphyllum rostratum</i> (Bedd.) Tagawa	Mainland China: Yunnan province; Shui 80676 (PE)	GU126697	GU126716	GU126727	-	-	-
<i>Lemmaphyllum rostratum</i> (Bedd.) Tagawa	Hainan Island; Wei XP et al. wxp108 (PE)	KX891376	KX891407	KX891363	-	KX891390	MF450477
<i>Lemmaphyllum squamatum</i> (A.R. Smith & X.C. Zhang) Li Wang	Mainland China: Guangxi province; W.B. Xu 07087 (PE)	GU126692	GU126710	GU126721	-	GU126699	-
<i>Lemmaphyllum squamatum</i> (A.R. Smith & X.C. Zhang) Li Wang	Mainland China: Guangxi province; Zhang XC 3925 (PE)	KX891378	KX891408	KX891365	-	KX891392	-
<i>Lepidomicrosorium buergerianum</i> (Miq.) Ching & K.H. Shing	Mainland China: Sichuan province; Lu SG-QC14 (PYU)	EU363247	EU363260	-	-	-	-
<i>Lepidomicrosorium buergerianum</i> (Miq.) Ching & K.H. Shing	Mainland China: Yunnan province; Shui 80894 (PE)	GQ256315	GQ256392	GQ256242	-	GQ256156	-
<i>Lepidomicrosorium subhemionitideum</i> (H.Christ) P.S. Wang	Mainland China: Yunnan province; D.Li 80 (PE)	-	GU126711	GU126722	-	GU126700	-
<i>Lepidomicrosorium subhemionitideum</i> (H.Christ) P.S. Wang	Mainland China: Guangxi province; Zhang 4111 (PE)	GU126693	GU126712	GU126723	-	GU126701	-
<i>Lepidomicrosorium superficiale</i> (Blume) L. Wang	Mainland China; Zhang XC 1290 (PE)	KX891379	KX891409	KX891366	-	KX891394	-
<i>Lepidomicrosorium superficiale</i> (Blume) L. Wang	Taiwan Islands; CC.Chen 1094 (H, HITBC)	MH665029	MH665092	MH665159	-	-	-
<i>Lepidomicrosorium superficiale</i> (Blume) L. Wang	Taiwan Islands; CC.Chen 1104 (HITBC)	MH051159	MH113458	MH113492	MH113525	MH113558	MH113591
<i>Lepidomicrosorium superficiale</i> (Blume) L. Wang	Taiwan Islands; Cranfill TW030 (UC)	EU482971	EU483022	GU126730	-	GU126708	-
<i>Lepidomicrosorium superficiale</i> (Blume) L. Wang	Japan Islands; Wade 3645 (TAIF)	MH665030	-	-	-	-	-
<i>Lepidomicrosorium superficiale</i> (Blume) L. Wang	Taiwan Islands; Cranfill TW073 (UC)	AY362568	AY362641	-	-	-	-
<i>Lepidomicrosorium superficiale</i> (Blume) L. Wang	Taiwan Islands; CC.Chen 1102 (H, HITBC)	MH051158	MH113457	MH113491	MH113524	MH113557	MH113590
<i>Lepidomicrosorium superficiale</i> (Blume) L. Wang	Indonesia Islands; Java; Wade 1913 (TAIF)	MH051160	MH113459	MH113493	MH113526	MH113559	MH113592
<i>Lepidomicrosorium superficiale</i> (Blume) L. Wang	Mainland China: Yunnan province; SG Lu s.n.	AY725055	AY725048	AY725049	-	-	-
<i>Lepidomicrosorium superficiale</i> (Blume) L. Wang	Mainland China: Yunnan province; Kuo 2915 (TAIF)	MH051161	MH113460	MH113494	MH113527	MH113560	MH113593
<i>Lepisorus accedens</i> (Blume) Hosok.	Philippine Islands; Kuo LY kuo2072 (TAI)	KX891368	KX891401	KX891354	-	KX891382	-
<i>Lepisorus accedens</i> (Blume) Hosok.	Philippine Islands; FJ11-129 Schneider H (BM)	KX891369	KX891400	KX891353	-	KX891381	-
<i>Lepisorus affinis</i> Ching	cult. SZBG; Zhang 4219 (PE)	GQ256256	GQ256328	GQ256173	-	GQ256086	-
<i>Lepisorus albertii</i> (Regel) Ching	Mainland China: Xinjiang province; Zhang 4325 (PE)	GQ256257	GQ256329	GQ256174	-	GQ256087	-
<i>Lepisorus angustus</i> Ching	Tibetan Plateau; Shen Z.H. S25 (PE)	GQ256290	GQ256364	GQ256214	-	GQ256127	-
<i>Lepisorus annamensis</i> (C.Chr.) Li Wang	Indonesia Islands; East Kalimantan; Hovenkamp 05-277 (L)	EU482931	EU482976	EU483025	-	-	-
<i>Lepisorus annamensis</i> (C.Chr.) Li Wang	Hainan Island; D Li 873 (PE)	GQ256252	GQ256324	GQ256166	-	GQ256079	-
<i>Lepisorus annuifrons</i> (Makino) Ching	Japan Islands; Kyoto Kokubo s.n. (TI)	GQ256258	GQ256331	GQ256176	-	GQ256089	-
<i>Lepisorus asterolepis</i> (Baker) Ching ex S.X. Xu	Mainland China: Sichuan province; Zhang 5171 (PE)	GQ256259	GQ256332	GQ256177	-	GQ256090	-
<i>Lepisorus bampsii</i> (Pic. Serm.) Zink	Africa Continent; R. Viane 11233 (PE)	GQ256260	GQ256333	GQ256178	-	GQ256091	-
<i>Lepisorus bicolor</i> (Takeda) Ching	Tibetan Plateau; Zhang 5157 (PE)	GQ256261	GQ256334	GQ256179	-	GQ256092	-
<i>Lepisorus boninensis</i> (Christ) Ching	cult. TBG acc.54022 [Japan Islands]	GQ256262	GQ256335	GQ256180	-	GQ256093	-
<i>Lepisorus clathratus</i> (C.B.Clarke) Ching	Mainland China: Yunnan province; Zhang 4533 (PE)	GQ256263	GQ256336	GQ256181	-	GQ256110	-
<i>Lepisorus clathratus</i> (C.B.Clarke) Ching	Mainland China: Yunnan province; Zhang 4515 (PE)	GQ256275	GQ256349	GQ256197	-	GQ256094	-
<i>Lepisorus clathratus</i> (C.B.Clarke) Ching	Tibetan Plateau; Dickoré 12430 (GOET)	DQ642154	DQ642192	DQ642236	-	-	-
<i>Lepisorus clathratus</i> (C.B.Clarke) Ching	Mainland China: Beijing; jingB-1 (PE)	KY419704*	KY419704*	KY419704*	KY419704*	KY419704*	KY419704*
<i>Lepisorus confluent</i> W.M. Chu	Mainland China: Yunnan province; C.D. Xu s.n. (PE)	GQ256264	GQ256337	GQ256182	-	GQ256095	-
<i>Lepisorus contortus</i> (Christ) Ching	Mainland China: Shanxi province; Q.R. Liu (PE)	GQ256266	GQ256339	GQ256184	-	GQ256098	-
<i>Lepisorus contortus</i> (Christ) Ching	Tibetan Plateau; Zhang 4699 (PE)	GQ256308	GQ256384	GQ256235	-	GQ256148	-
<i>Lepisorus elegans</i> Ching ex W.M. Chu	Mainland China: Yunnan province; Zhang 4444 (PE)	GQ256268	GQ256342	GQ256187	-	GQ256100	-
<i>Lepisorus excavatus</i> (Willd.) Ching	Africa Continent; Tanzania; Hemp 3561 (DSM)	DQ642155	DQ642193	GQ256189	-	GQ256101	-
<i>Lepisorus excavatus</i> (Willd.) Ching	Grande Comore Island; Rakotondrainibe 6785 (P)	DQ642156	DQ642194	GQ256188	-	GQ256102	-
<i>Lepisorus hachioensis</i> Sa. Kurata	Japan Islands; Zhang 4358 (PE)	GQ256269	GQ256343	GQ256190	-	GQ256103	-
<i>Lepisorus henryi</i> (Hieron. ex C.Chr.) Li Wang	Mainland China: Yunnan province; Shui 80679 (PE)	GQ256253	GQ256325	GQ256167	-	GQ256080	-
<i>Lepisorus heterolepis</i> (Rosenst.) Ching	Tibetan Plateau; Zhang 5064 (PE)	GQ256270	GQ256344	GQ256191	-	GQ256104	-
<i>Lepisorus hsiaowataiensis</i> Ching & S.K. Wu	Mainland China: Hebei province; Q.R. Liu (PE)	GQ256271	GQ256345	GQ256192	-	GQ256105	-
<i>Lepisorus kawakamii</i> (Hayata) Tagawa	Taiwan Islands; Ranker 2051 (COLO)	EU482940	EU482990	GQ256193	-	GQ256106	-
<i>Lepisorus kuchensis</i> (Y.C. Wu) Ching	Mainland China: Guangxi province; J.M. Xi 08188 (PE)	GQ256272	GQ256346	GQ256194	-	GQ256107	-
<i>Lepisorus lewisii</i> (Baker) Ching	Mainland China: Anhui province; Y Liu 05620 (PE)	GQ256273	GQ256347	GQ256195	-	GQ256108	-
<i>Lepisorus likiangensis</i> Ching & S.K. Wu	Mainland China: Yunnan province; Zhang 4468 (PE)	GQ256303	GQ256379	GQ256230	-	GQ256099	-
<i>Lepisorus likiangensis</i> Ching & S.K. Wu	Mainland China: Yunnan province; Zhang 4488 (PE)	GQ256267	GQ256341	GQ256186	-	GQ256109	-
<i>Lepisorus likiangensis</i> Ching & S.K. Wu	Tibetan Plateau; Zhang 5117 (PE)	GQ256274	GQ256348	GQ256196	-	GQ256143	-

<i>Lepisorus lineariformis</i> Ching & S.K. Wu	Tibetan Plateau; Zhang 4771 (PE)	GQ256276	GQ256350	GQ256198	-	GQ256111	-
<i>Lepisorus lineariformis</i> Ching & S.K. Wu	Mainland China: Yunnan province; Zhang 4437 (PE)	GQ256277	GQ256351	GQ256199	-	GQ256112	-
<i>Lepisorus loriformis</i> (Wall. ex Mett.) Ching	Mainland China: Yunnan province; Zhang 4440 (PE)	GQ256280	GQ256352	GQ256201	-	GQ256114	-
<i>Lepisorus loriformis</i> var. <i>steniste</i> (C.B. Clarke) Ching	Tibetan Plateau; Z.D. Fang XZ-412 (PE)	GQ256279	GQ256353	GQ256202	-	GQ256115	-
<i>Lepisorus luchunensis</i> Y.X. Lin	Mainland China: Yunnan province; Qi 097 (PE)	HQ712000	HQ712008	HQ712019	-	HQ712007	-
<i>Lepisorus macrospheus</i> (Baker) Ching	Tibetan Plateau; Zhang 4794 (PE)	GQ256280	GQ256354	GQ256203	-	GQ256116	-
<i>Lepisorus macrospheus</i> (Baker) Ching	cult. KBG; Kim 2012-3 (KUN)	JX103697	JX103739	JX103781	-	JX103655	-
<i>Lepisorus macrospheus</i> (Baker) Ching	Taiwan Islands; Cranfill TW018 (UC)	EU482941	EU482991	EU483036	-	-	-
<i>Lepisorus marginatus</i> Ching	Mainland China: Hubei province; Zhang 3360 (PE)	GQ256281	GQ256355	GQ256204	-	GQ256117	-
<i>Lepisorus medogensis</i> Ching & Y.X. Lin	Tibetan Plateau; Z.D. Fang XZ-266 (PE)	GQ256282	GQ256356	GQ256205	-	GQ256118	-
<i>Lepisorus megasorus</i> (C. Chr.) Ching	Taiwan Islands; Cranfill TW069 (UC)	DQ642158	DQ642196	GQ256206	-	GQ256119	-
<i>Lepisorus miyoshianus</i> (Makino) Fraser-Jenk. & Subh. Chandra	Taiwan Islands; Cranfill TW087 (UC)	AY362563	AY362630	DQ179640	-	-	-
<i>Lepisorus miyoshianus</i> (Makino) Fraser-Jenk. & Subh. Chandra	Mainland China: Sichuan province; C.C. Liu DB06104 (PE)	GQ256255	GQ256327	GQ256172	-	GQ256085	-
<i>Lepisorus monilisorus</i> (Hayata) Tagawa	Taiwan Islands; E. Schuettpelz 1136A (DUKE)	-	-	-	KF909068	-	KF909023
<i>Lepisorus monilisorus</i> (Hayata) Tagawa	Taiwan Islands; Cranfill TW012 (UC)	EU482942	EU482992	EU483037	-	-	-
<i>Lepisorus monilisorus</i> (Hayata) Tagawa	Taiwan Islands; H.M. Zhang 20050117 (PE)	GQ256283	GQ256357	GQ256207	-	GQ256120	-
<i>Lepisorus morrissonensis</i> (Hayata) H. Itô	Tibetan Plateau; Zhang 5113 (PE)	GQ256284	GQ256358	GQ256208	-	GQ256121	-
<i>Lepisorus morrissonensis</i> (Hayata) H. Itô	Tibetan Plateau; Zhang 4736 (PE)	GQ256285	GQ256359	GQ256209	-	GQ256122	-
<i>Lepisorus mucronatus</i> (Fée) Li Wang	Malaysia; Jaman 5891 (UC)	AY362562	AY362629	GQ256168	-	GQ256081	-
<i>Lepisorus obscurevenulosus</i> (Hayata) Ching	Mainland China: Guangxi province; Zhang 4151 (PE)	GQ256286	GQ256360	GQ256210	-	GQ256123	-
<i>Lepisorus oligolepidus</i> (Baker) Ching	Tibetan Plateau; Zhang 5082 (PE)	GQ256287	GQ256361	GQ256211	-	GQ256124	-
<i>Lepisorus onoei</i> (Franch. & Sav.) Ching	Japan Islands; Zhang 4352 (PE)	GQ256288	GQ256362	GQ256212	-	GQ256125	-
<i>Lepisorus patungensis</i> Ching & S.K. Wu	Mainland China: Hubei province; Zhang 3413 (PE)	GQ256289	GQ256363	GQ256213	-	GQ256126	-
<i>Lepisorus platyrhynchos</i> (Kunze) Li Wang	cult. BGZ; Kreier s.n. (GOET)	DQ642152	DQ642190	DQ642233	-	GQ256082	-
<i>Lepisorus pseudonodus</i> Ching	Mainland China: Sichuan province; Zhang 4249 (PE)	GQ256291	GQ256365	GQ256215	-	GQ256128	-
<i>Lepisorus pseudoussuriensis</i> Tagawa	Taiwan Islands; Cranfill TW093 (UC)	EU482943	EU482993	GQ256216	-	GQ256129	-
<i>Lepisorus pumilus</i> Ching & S.K. Wu	Mainland China: Gansu province; M.Z. Wang 60667 (PE)	GQ256292	GQ256366	GQ256217	-	GQ256130	-
<i>Lepisorus rotundus</i> Ching	Africa Continent: Tanzania; RV 7675	HQ711996	HQ712012	HQ712015	-	HQ712006	-
<i>Lepisorus schraderi</i> (Mett.) Ching	Reunion Island; RV 8253	HQ711998	HQ712010	HQ712016	-	HQ712002	-
<i>Lepisorus scolopendrium</i> (Ching) Mehra & Bir	Indochina: Laos; Wu 2441 (KUN)	JX103698	JX103740	JX103782	-	JX103656	-
<i>Lepisorus scolopendrium</i> (Ching) Mehra & Bir	Tibetan Plateau; Zhang 4659 (PE)	GQ256294	GQ256368	GQ256219	-	GQ256133	-
<i>Lepisorus scolopendrium</i> (Ching) Mehra & Bir	Tibetan Plateau; Y.D. Tang YD-076 (PE)	GQ256295	GQ256369	GQ256220	-	GQ256132	-
<i>Lepisorus sinensis</i> (Christ) Ching	Mainland China: Yunnan province; Shui 81069 (PE)	GQ256296	GQ256370	GQ256221	-	GQ256134	-
<i>Lepisorus sordidus</i> (C. Chr.) Ching	Mainland China: Yunnan province; Zhang 3218 (PE)	GQ256298	GQ256372	GQ256223	-	GQ256135	-
<i>Lepisorus sordidus</i> (C. Chr.) Ching	Mainland China: Sichuan province; Zhang 0612(PE)	GQ256297	GQ256371	GQ256222	-	GQ256136	-
<i>Lepisorus spicatus</i> (L.f.) Li Wang	cult. BGG; Schneider s.n. (GOET)	DQ642153	DQ642191	DQ642234	-	-	-
<i>Lepisorus spicatus</i> (L.f.) Li Wang	Tahiti Island; Ranker 1915 (COLO)	-	-	-	EF463800	EF463490	-
<i>Lepisorus subconfluens</i> Ching	Mainland China: Yunnan province; Zhang 4518 (PE)	GQ256299	GQ256373	GQ256224	-	GQ256137	-
<i>Lepisorus sublinearis</i> (Baker ex Takeda) Ching	Mainland China: Yunnan province; Shui 80595 (PE)	GQ256300	GQ256374	GQ256225	-	GQ256139	-
<i>Lepisorus sublinearis</i> (Baker ex Takeda) Ching	Mainland China: Yunnan province; Shui 81060 (PE)	GQ256301	GQ256375	GQ256226	-	GQ256138	-
<i>Lepisorus thaipaiensis</i> Ching & S.K. Wu	Mainland China: Shanxi province; G.Y. Rao 2005-045A (PE)	GQ256302	GQ256378	GQ256229	-	GQ256142	-
<i>Lepisorus thunbergianus</i> (Kaulf.) Ching	Mainland China: Chongqing; Zhang 5205 (PE)	GQ256305	GQ256381	GQ256232	-	GQ256144	-
<i>Lepisorus thunbergianus</i> (Kaulf.) Ching	Mainland China: Yunnan province; Zhang 4544 (PE)	GQ256306	GQ256382	GQ256233	-	GQ256146	-
<i>Lepisorus thunbergianus</i> (Kaulf.) Ching	Japan Islands; Koichi Ohora 2005042404 (TI)	GQ256304	GQ256380	GQ256231	-	GQ256145	-
<i>Lepisorus tibeticus</i> Ching & S.K. Wu	Tibetan Plateau; Zhang 4694 (PE)	GQ256307	GQ256383	GQ256234	-	GQ256147	-
<i>Lepisorus tosaensis</i> (Makino) H. Itô	Japan Islands; Sayumi Fujimoto 2005042904 (TI)	GQ256309	GQ256385	GQ256236	-	GQ256149	-
<i>Lepisorus uchiyamae</i> (Makino) H. Itô	Japan Islands; Sayumi Fujimoto 2005042902 (TI)	GQ256310	GQ256386	GQ256237	-	GQ256150	-
<i>Lepisorus ussuriensis</i> (Regel & Maack) Ching	Mainland China: Heilongjiang province; B.D. Liu s.n. (PE)	GQ256311	GQ256387	GQ256238	-	GQ256151	-
<i>Lepisorus ussuriensis</i> var. <i>distans</i> (Makino) Tagawa	Japan Islands; Sayumi Fujimoto SF05051602 (TI)	GQ256312	GQ256388	GQ256239	-	GQ256152	-
<i>Lepisorus validinervis</i> (Kunze) Li Wang	Borneo Island; Daniele Cicuzza 2205 (UBDH)	MH665031	MH665093	MH665160	MH664989	MH665005	MH665019
<i>Lepisorus xiphiopteris</i> (Baker) W.M. Chu ex Y.X. Lin	Mainland China: Yunnan province; C.D. Xu A0303 (PE)	GQ256313	GQ256389	GQ256240	-	GQ256153	-

<i>Leptochilus axillaris</i> (Cav.) Kaulf.	Indochina: Laos; Wu 2344 (KUN)	JX103699	JX103741	JX103783	-	JX103657	-
<i>Leptochilus axillaris</i> (Cav.) Kaulf.	Indochina: Laos; Wu 2439 (KUN)	JX103700	JX103742	JX103784	-	JX103658	-
<i>Leptochilus axillaris</i> (Cav.) Kaulf.	Indochina: Laos; Wu 2462 (KUN)	JX103701	JX103743	JX103785	-	JX103659	-
<i>Leptochilus cantoniensis</i> (Baker) Ching	Mainland China; Dong 743 (PE)	EU482946	EU482996	EU483042	-	-	-
<i>Leptochilus cantoniensis</i> (Baker) Ching	Mainland China; Dong 172 (PE)	EU482945	EU482995	EU483041	-	-	-
<i>Leptochilus cantoniensis</i> (Baker) Ching	cult. KBCC K032796 [Hainan Island]; (H)	MH665032	MH665094	MH665161	-	-	-
<i>Leptochilus cantoniensis</i> (Baker) Ching	Hainan Island; Kuo 1701 (TAIF)	-	MH665095	MH665162	-	-	-
<i>Leptochilus cf. decurrens</i>	Mainland China: Yunnan province; RBGE 19933707 (PE)	MH665033	MH665096	MH665163	-	-	-
<i>Leptochilus decurrens</i> Blume	Indonesia Islands: Java; Douglas 28 (UC)	AY096203	AY096228	DQ179640	-	-	-
<i>Leptochilus decurrens</i> Blume	cult. KBG; X.Y. Du 1003 (KUN)	-	-	-	-	HQ597027	-
<i>Leptochilus decurrens</i> Blume	cult. KBG; Kim 2012-12 (KUN)	JX103724	JX103766	JX103808	-	JX103682	-
<i>Leptochilus digitatus</i> (Baker) Noot.	Mainland China; Zhang 3509 (PE)	EU482947	EU482997	EU483043	-	-	-
<i>Leptochilus digitatus</i> (Baker) Noot.	Indochina: Vietnam; A.R. Smith 00-036 (UC)	EU482948	EU482998	EU483044	-	-	-
<i>Leptochilus digitatus</i> (Baker) Noot.	Indochina: Vietnam; Chao 1556 (TAIF)	MH665034	MH665097	MH665164	-	-	-
<i>Leptochilus digitatus</i> (Baker) Noot.	Hainan Island; Kuo 1771 (TAIF)	-	MH665098	MH665165	-	-	-
<i>Leptochilus digitatus</i> (Baker) Noot.	cult. KBCC K020955 [Indochina: Vietnam]; (H)	MH665035	MH665099	MH665166	-	-	-
<i>Leptochilus digitatus</i> (Baker) Noot.	Indochina: Laos; Wu 2515 (KUN)	JX103695	JX103737	JX103779	-	JX103653	-
<i>Leptochilus digitatus</i> (Baker) Noot.	cult. XTBG; CC.Chen 1067 (H)	MH051162	MH113461	MH113495	MH113528	MH113561	MH113594
<i>Leptochilus ellipticus</i> (Thunb. ex Murray) Noot.	Mainland China: Yunnan province; Lin GX 003 (PE)	MH665036	MH665100	MH665167	-	-	-
<i>Leptochilus ellipticus</i> (Thunb. ex Murray) Noot.	Japan Islands; Wade 3656 (TAIF)	MH665037	MH665101	MH665168	-	-	-
<i>Leptochilus ellipticus</i> (Thunb. ex Murray) Noot.	Mainland China; Zhang 1923 (PE)	EU482949	EU482999	EU483045	-	-	-
<i>Leptochilus cf. ellipticus</i>	cult. XTBG; CC.Chen 1065 (H)	MH665038	MH665102	MH665169	-	-	-
<i>Leptochilus cf. ellipticus</i>	Mainland China: Yunnan province; Schneider 2011 V191 (PE)	MH665039	MH665103	MH665170	-	-	-
<i>Leptochilus cf. ellipticus</i>	Mainland China: Yunnan province; Schneider 2011 V013 (PE)	MH665040	MH665104	MH665171	-	-	-
<i>Leptochilus cf. ellipticus</i>	cult. XTBG; CC.Chen 1068 (H)	MH665041	MH665105	MH665172	-	-	-
<i>Leptochilus ellipticus</i> var. <i>flexilobus</i> (Christ) X.C. Zhang	Mainland China: Guangxi province; Wade 2518 (TAIF)	MH665042	MH665106	MH665173	-	-	-
<i>Leptochilus ellipticus</i> var. <i>flexilobus</i> (Christ) X.C. Zhang	cult. KBCC K032967 [Hainan Island]; (H)	-	MH665107	MH665174	-	-	-
<i>Leptochilus ellipticus</i> var. <i>pentaphyllus</i> (Baker) X.C. Zhang & <i>Leptochilus ellipticus</i> var. <i>pentaphyllus</i> (Baker) X.C. Zhang & <i>Leptochilus hemionitideus</i> (C. Presl) Noot.	Mainland China: Yunnan province; Xu A0357 (PE)	MH665043	MH665108	MH665175	-	-	-
<i>Leptochilus hemionitideus</i> (C. Presl) Noot.	Mainland China: Yunnan province, Ruili; SG Lu-SG9 (PYU)	EU363242	EU363255	-	-	-	-
<i>Leptochilus hemionitideus</i> (C. Presl) Noot.	cult. XTBG; CC.Chen 1066 (H)	MH051165	MH113464	MH175521	MH113531	MH113564	MH113597
<i>Leptochilus hemionitideus</i> (C. Presl) Noot.	Indochina: Laos; Wu 2437 (KUN)	JX103694	JX103736	JX103778	-	JX103652	-
<i>Leptochilus hemionitideus</i> (C. Presl) Noot.	Taiwan Islands; CC.Chen 1015 (H)	MH051164	MH113463	MH113497	MH113530	MH113563	MH113596
<i>Leptochilus x hemitomus</i> (Hance) Noot.	Mainland China; Zhang 3302 (PE)	EU482951	EU483001	EU483047	-	-	-
<i>Leptochilus henryi</i> (Baker) X.C. Zhang	Mainland China: Sichuan province; Zhang 2541 (PE)-1	EU482952	EU483002	EU483048	-	GU126709	-
<i>Leptochilus henryi</i> (Baker) X.C. Zhang	Mainland China: Sichuan province; Zhang 2541 (PE)-2	GQ256254	GQ256326	GQ256171	-	GQ256084	-
<i>Leptochilus henryi</i> (Baker) X.C. Zhang	cult. XTBG; CC.Chen 1072 (H)	MH665044	MH665109	MH665176	-	-	-
<i>Leptochilus heterophyllus</i> (S.K. Wu & K.L. Phan) Christenh.	Indochina: Vietnam; WP-135 (KUN)	JX103688	JX103730	JX103772	-	JX103646	-
<i>Leptochilus heterophyllus</i> (S.K. Wu & K.L. Phan) Christenh.	Indochina: Vietnam; WP-136 (KUN)	JX520933	JX520935	JX520937	-	JX520931	-
<i>Leptochilus heterophyllus</i> (S.K. Wu & K.L. Phan) Christenh.	Indochina: Vietnam; WP-201 (KUN)	JX520934	JX520936	JX520938	-	JX520932	-
<i>Leptochilus heterophyllus</i> (S.K. Wu & K.L. Phan) Christenh.	Mainland China: Yunnan province; P.11226 B (PE)	MH665045	MH665110	MH665177	-	-	-
<i>Leptochilus heterophyllus</i> (S.K. Wu & K.L. Phan) Christenh.	Mainland China: Yunnan province; P.11226 A (PE)	MH665046	MH665111	MH665178	-	-	-
<i>Leptochilus leveillei</i> (Christ) X.C. Zhang & Noot.	Mainland China: Sichuan province, Mt. Emei; SG Lu-EM26 (PYU)	EU363240	EU363254	-	-	-	-
<i>Leptochilus leveillei</i> (Christ) X.C. Zhang & Noot.	Mainland China: Yunnan province; Zhang 4312 (PE)	MH665047	MH665112	MH665179	-	-	-
<i>Leptochilus cf. leveillei</i>	cult. XTBG; CC.Chen 1070 (H)	MH051166	MH113465	MH113498	MH113532	MH113565	MH113598
<i>Leptochilus longipes</i> (Ching) X.C. Zhang	Indochina: Vietnam; Wade 2615 (TAIF)	MH665048	MH665113	MH665180	-	-	-
<i>Leptochilus longipes</i> (Ching) X.C. Zhang	Indochina: Vietnam; Wade 4102 (TAIF)	MH665049	MH665114	MH665181	-	-	-
<i>Leptochilus longipes</i> (Ching) X.C. Zhang	Mainland China: Guangxi province; Wade 2517 (TAIF)	MH665050	MH665115	MH665182	-	-	-
<i>Leptochilus macrophyllus</i> (Blume) Noot.	Indonesia Islands: Java; Wade 1962 (TAIF)	MH051167	MH113466	MH113499	MH113533	MH113566	MH113599
<i>Leptochilus macrophyllus</i> (Blume) Noot.	Philippine Islands; Wade 3798 (TAIF)	-	MH665116	MH665183	-	-	-
<i>Leptochilus macrophyllus</i> (Blume) Noot.	Solomon Islands; Wade 2776 (TAIF)	MH665051	MH665117	MH665184	-	-	-
<i>Leptochilus macrophyllus</i> (Blume) Noot.	Solomon Islands; Wade 2845 (TAIF)	MH665052	MH665118	MH665185	-	-	-

<i>Leptochilus pedunculatus</i> (Hook. & Grev.) Fraser-Jenk.	Indochina: Vietnam; Wade 1334 (TAIF)	MH051168	MH113467	MH113500	MH113534	MH113567	MH113600
<i>Leptochilus pothifolius</i> (Buch.-Ham. ex D. Don) Fraser-Jenk.	Japan Islands; Wade 3681 (TAIF)	MH665053	MH665119	MH665186	-	-	-
<i>Leptochilus pothifolius</i> (Buch.-Ham. ex D. Don) Fraser-Jenk.	Taiwan Islands; CC.Chen 1017 (H)	MH051163	MH113462	MH113496	MH113529	MH113562	MH113595
<i>Leptochilus pothifolius</i> (Buch.-Ham. ex D. Don) Fraser-Jenk.	Mainland China: Yunnan province; Zhang 4231 (PE)	MH665054	MH665120	MH665187	-	-	-
<i>Leptochilus pothifolius</i> (Buch.-Ham. ex D. Don) Fraser-Jenk.	Mainland China: Yunnan province; Zhang 4207 (PE)	MH665055	MH665121	MH665188	-	-	-
<i>Leptochilus pothifolius</i> (Buch.-Ham. ex D. Don) Fraser-Jenk.	Mainland China: Guangxi province; Wade 2519 (TAIF)	MH665056	MH665122	MH665189	-	-	-
<i>Leptochilus pothifolius</i> (Buch.-Ham. ex D. Don) Fraser-Jenk.	Indochina: Laos; Wu 2712 (KUN)	JX103696	JX103738	JX103780	-	JX103654	-
<i>Leptochilus cf. pothifolius</i>	Mainland China: Yunnan province; Zhang 4356 (PE)	MH665057	MH665123	MH665190	-	-	-
<i>Leptochilus cf. pothifolius</i>	Mainland China: Yunnan province; CC.Chen 1112 (HITBC)	MH665058	MH665124	MH665191	MH664990	MH665006	-
<i>Leptochilus cf. pothifolius</i>	Mainland China: Yunnan province; CC.Chen 1113 (HITBC)	MH665059	MH665125	MH665192	MH664991	MH665007	MH665020
<i>Leptochilus pteropus</i> (Blume) Fraser-Jenk.	cult. BGG; Kreier s.n. (GOET)	EU482965	EU483016	EU483061	-	-	-
<i>Leptochilus pteropus</i> (Blume) Fraser-Jenk.	Mainland China: Yunnan province; Zhang 4225 (PE)	MH665060	MH665126	MH665193	-	-	-
<i>Leptochilus pteropus</i> (Blume) Fraser-Jenk.	Taiwan Islands; CC.Chen 1010 (H)	MH051176	MH113475	MH113508	MH113542	MH113575	MH113608
<i>Leptochilus x shintenensis</i> (Hayata) X.C. Zhang & Noot.	cult. KBCC K017274 [Taiwan Islands]	MH051169	MH113468	MH113501	MH113535	MH113568	MH113601
<i>Leptochilus simplifrons</i> (H. Christ) Tagawa	cult. JNU; Zhang 3800 (PE)	EU482953	EU483003	EU483049	-	-	-
<i>Leptochilus wrightii</i> (Hook. & Baker) X.C. Zhang	cult. KBG; Kim 2012-15 (KUN)	JX103727	JX103769	JX103811	-	JX103685	-
<i>Leptochilus wrightii</i> (Hook. & Baker) X.C. Zhang	Taiwan Islands; Li 596 (TAIF)	-	-	-	JF304021	-	JF303959
<i>Leptochilus wrightii</i> (Hook. & Baker) X.C. Zhang	Taiwan Islands; CC.Chen 1087 (H)	MH051170	MH113469	MH113502	MH113536	MH113569	MH113602
<i>Leptochilus wrightii</i> (Hook. & Baker) X.C. Zhang	cult. KBCC K015603 [Taiwan Islands]; (H)	MH665061	MH665127	MH665194	-	-	-
<i>Leptochilus wrightii</i> (Hook. & Baker) X.C. Zhang	Japan Islands; Tsutsumi 1067 (CT)	EU482954	EU483004	EU483050	-	-	-
<i>Leptochilus wrightii</i> (Hook. & Baker) X.C. Zhang	Taiwan Islands; CC.Chen 1016 (H)	MH665062	MH665128	MH665195	-	-	-
<i>Leptochilus wrightii</i> (Hook. & Baker) X.C. Zhang	cult. KBCC K015605 [Taiwan Islands]; (H)	MH665063	MH665129	MH665196	-	-	-
<i>Leptochilus wrightii</i> (Hook. & Baker) X.C. Zhang	Mainland China: Yunnan province; Li 47 (PE)	MH665064	MH665130	MH665197	-	-	-
<i>Leptochilus cf. wrightii</i>	Mainland China: Yunnan province; Schneider 2011 V163 (PE)	MH665065	MH665131	MH665198	-	-	-
<i>Leptochilus sp.</i>	Japan Islands; Wade 3657 (TAIF)	MH665066	MH665132	MH665199	-	-	-
<i>Leptochilus sp.</i>	cult. XTBG; CC.Chen 1071 (H)	MH665067	MH665133	MH665200	-	-	-
<i>Microsorium biseriatum</i> (Bosman) Noot.	Solomon Islands; Wade 2735 (TAIF)	MH051189	MH113488	MH113521	MH113554	MH113587	MH113621
<i>Microsorium commutatum</i> (Bl.) Copel.	Solomon Islands; Wade 2810 (TAIF)	MH665068	MH665134	MH665201	-	-	-
<i>Microsorium commutatum</i> (Bl.) Copel.	Admiralty Islands; Wagner & Grether 3481 (UC)	AY362571	-	-	-	-	-
<i>Microsorium commutatum</i> (Bl.) Copel.	cult. Whitehead; A.R. Smith 2901 (UC)	-	EU483005	EU483051	-	-	-
<i>Microsorium commutatum</i> (Bl.) Copel.	Philippine Islands; Wade 3768 (TAIF)	MH051171	MH113470	MH113503	MH113537	MH113570	MH113603
<i>Microsorium cuspidatum</i> (D. Don) Tagawa	cult. LBG 3560	AF470335	-	AY083638	-	-	-
<i>Microsorium cuspidatum</i> (D. Don) Tagawa	cult. source (UC)	-	AY096230	-	-	-	-
<i>Microsorium cuspidatum</i> (D. Don) Tagawa	cult. KBG; X.Y.Du 1002 (KUN)	-	-	-	-	HQ597026	-
<i>Microsorium cuspidatum</i> (D. Don) Tagawa	cult. KBG; Kim 2012-14 (KUN)	JX103726	JX103768	JX103810	-	JX103684	-
<i>Microsorium cuspidatum</i> (D. Don) Tagawa	cult. KBG; Kim 2012-6 (KUN)	JX103707	JX103749	JX103791	-	JX103665	-
<i>Phymatosorus cuspidatus</i> [= <i>M. cuspidatum</i>] subsp. <i>beddomei</i>	South of Indian subcontinent; FN132 (TAIF)	MH665069	MH665135	MH665202	MH664992	-	-
<i>Microsorium glossophyllum</i> Copel.	Solomon Islands; Wade 2782 (TAIF)	MH051179	MH113478	MH113511	MH113545	MH113578	MH113611
<i>Microsorium glossophyllum</i> Copel.	Solomon Islands; Wade 3053 (TAIF)	MH051180	MH113479	MH113512	MH175522	MH113579	MH113612
<i>Microsorium grossum</i> (Langsd. & Fisch.) S.B. Andrews	Solomon Islands; Wade 2910 (TAIF)	MH665070	MH665136	MH665203	-	-	-
<i>Microsorium grossum</i> (Langsd. & Fisch.) S.B. Andrews	Hawaiian Islands; Lorence 9155 (DL)	EU482956	EU483007	EU483053	-	-	-
<i>Microsorium grossum</i> (Langsd. & Fisch.) S.B. Andrews	Moorea Island; Ranker 1941(COLO)	-	-	-	EF463831	EF463500	-
<i>Microsorium grossum</i> (Langsd. & Fisch.) S.B. Andrews	Moorea Island; Ranker 1941(COLO)	DQ179633	DQ179636	DQ179642	-	-	-
<i>Microsorium hainanense</i> Noot.	Hainan Island; Lu SG-V73 (PYU)	EU363249	EU363263	-	-	-	-
<i>Microsorium heterocarpum</i> Ching	Philippine Islands; Wade 3758 (TAIF)	MH665071	MH665137	-	-	-	-
<i>Microsorium heterocarpum</i> Ching	Borneo Island; Daniele Cicuzza 2203 (UBDH)	MH665072	MH665138	MH665204	MH664993	MH665008	MH665021
<i>Microsorium insigne</i> (Blume) Copel.	Indonesia Islands; Java; Wade 2059 (TAIF)	MH665073	MH665139	MH665205	-	-	-
<i>Microsorium insigne</i> (Blume) Copel.	Indochina: Laos; Wu 2435 (KUN)	JX103703	JX103745	JX103787	-	JX103661	-
<i>Microsorium insigne</i> (Blume) Copel.	Mainland China: Yunnan province; CC.Chen 1116 (HITBC)	MH665074	MH665140	MH665206	MH664994	MH665009	-
<i>Microsorium insigne</i> (Blume) Copel.	Indochina: Thailand; Lu.P.F. 15695 (TAIF)	MH051173	MH113472	MH113505	MH113539	MH113572	MH113605
<i>Microsorium insigne</i> (Blume) Copel.	Indochina: Vietnam; WadeVN 072 (TAIF)	MH665075	MH665141	MH665207	-	-	-

<i>Microsorium insigne</i> (Blume) Copel.	Mainland China: Yunnan province; CC.Chen 1109 (HITBC)	MH665076	MH665142	MH665208	MH664995	MH665010	MH665022
<i>Microsorium insigne</i> (Blume) Copel.	cult. XTBG; CC.Chen 1073 (H)	MH051172	MH113471	MH113504	MH113538	MH113571	MH113604
<i>Microsorium insigne</i> (Blume) Copel.	Mainland China; Liu 204 (PE)	EU482957	EU483008	EU483054	-	-	-
<i>Microsorium insigne</i> (Blume) Copel.	Mainland China; Liu 214 (PE)	EU482958	EU483009	EU483055	-	-	-
<i>Microsorium insigne</i> (Blume) Copel.	Mainland China; Zhang 3510 (PE)	EU482959	EU483010	EU483056	-	-	-
<i>Microsorium lastii</i> (Baker) Tardieu	Perier 7937 (P)	EU482961	EU483012	EU483058	-	-	-
<i>Microsorium linguiforme</i> (Mett.) Copel.	New Guinea Island; T. Ranker 1776 (UC)	AF470334	-	AY083637	-	-	-
<i>Microsorium linguiforme</i> (Mett.) Copel.	Solomon Islands; Wade 2887 (TAIF)	MH051174	MH113473	MH113506	MH113540	MH113573	MH113606
<i>Microsorium membranaceum</i> (D.Don) Ching var. <i>membranaceum</i>	cult. Xishuanbanna; Li 95 (PE)	EU482962	EU483013	EU483059	-	-	-
<i>Microsorium membranaceum</i> (D.Don) Ching var. <i>membranaceum</i>	Taiwan Islands; Cranfill TW042 (UC)	EU482963	DQ642199	DQ642244	-	-	-
<i>Microsorium membranaceum</i> (D.Don) Ching var. <i>membranaceum</i>	Taiwan Islands; CC.Chen 1077 (H)	MH051175	MH113474	MH113507	MH113541	MH113574	MH113607
<i>Microsorium membranaceum</i> (D.Don) Ching var. <i>membranaceum</i>	cult. KBG; Kim 2012-2 (KUN)	JX103704	JX103746	JX103788	-	JX103662	-
<i>Microsorium membranaceum</i> (D.Don) Ching var. <i>membranaceum</i>	Mainland China: Yunnan province; SG Lu s.n.	AY725053	AY725047	AY725051	-	-	-
<i>Microsorium membranaceum</i> var. <i>carinatum</i> W.M.Chu & Z.R.He	Mainland China: Yunnan province; Shui YM et al. 80767	-	-	-	-	KX891393	-
<i>Microsorium membranaceum</i> var. <i>carinatum</i> W.M.Chu & Z.R.He	Mainland China: Yunnan province; SG Lu s.n.	AY725054	AY725046	AY725050	-	-	-
<i>Microsorium membranifolium</i> (R. Br.) Ching	Solomon Islands; Wade 2753 (TAIF)	MH665077	MH665143	MH665209	MH664996	MH665011	MH665023
<i>Microsorium membranifolium</i> (R. Br.) Ching	Hawaiian Islands; Dunn 458 (LOA)	EU482964	EU483014	EU483060	-	-	-
<i>Microsorium membranifolium</i> (R. Br.) Ching	cult. CBG; Wade 1824 (TAIF)	MH665078	MH665144	MH665210	MH664997	MH665012	MH665024
<i>Microsorium membranifolium</i> (R. Br.) Ching	cult. BGG; Schneider s.n. (GOET)	DQ642161	DQ642200	DQ642245	-	-	-
<i>Microsorium musifolium</i> (Blume) Copel.	cult. UCBG 58.0649 [Indonesia Islands: Java; (UC)]	AF470333	-	AY083636	-	-	-
<i>Microsorium musifolium</i> (Blume) Copel.	cult. KBCC K013621 [Indochina: Thailand]; (H)	MH665079	MH665145	MH665211	MH664998	MH665013	-
<i>Microsorium musifolium</i> (Blume) Copel.	cult. KBCC K013966 [Taiwan Islands]; (H)	MH665080	MH665146	MH665212	MH664999	-	-
<i>Microsorium novae-zealandiae</i> (Baker) Copel.	New Zealand Islands; Perrie et al. (WELT P20873)	DQ401116	DQ401126	DQ401121	-	-	-
<i>Microsorium novae-zealandiae</i> (Baker) Copel.	New Zealand Islands (WELT P20876; LRP3584)	DQ401120	-	DQ401124	-	-	-
<i>Microsorium papuanum</i> (Baker) Parris	cult. BGB; Schuettelpelz 603 (GOET)	DQ642162	EU483015	DQ642246	-	-	-
<i>Microsorium powellii</i> (Hook. & Baker) Copel.	Solomon Islands; Wade 3352 (TAIF)	MH665081	MH665147	MH665213	MH665000	MH665014	MH665025
<i>Microsorium cf. punctatum</i>	cult. BGH, Schneider s.n. (GOET)	DQ164444	DQ164475	DQ164508	-	-	-
<i>Microsorium punctatum</i> (L.) Copel.	Taiwan Islands; CC.Chen 1076 (H)	MH051178	MH113477	MH113510	MH113544	MH113577	MH113610
<i>Microsorium punctatum</i> (L.) Copel.	Indochina: Laos; Wu 2506 (KUN)	JX103705	JX103747	JX103789	-	JX103663	-
<i>Microsorium punctatum</i> (L.) Copel.	Indochina: Vietnam; Wade 1390 (TAIF)	MH051177	MH113476	MH113509	MH113543	MH113576	MH113609
<i>Microsorium punctatum</i> (L.) Copel.	Hainan Island; Zhang 4194 (PE)	GQ256316	GQ256394	GQ256244	-	GQ256158	-
<i>Microsorium punctatum</i> (L.) Copel.	cult. LBG 24091 [Philippine Islands; C. Ridsdale]	AF470337	-	AY083640	-	-	-
<i>Microsorium punctatum</i> (L.) Copel.	Taiwan Islands; Ranker 2096 (COLO)	EU482966	EU483017	EU483063	-	-	-
<i>Microsorium punctatum</i> (L.) Copel.	cult. RBGV; CC.Chen 1084 (H)	MH665082	MH665148	-	-	-	-
<i>Microsorium pustulatum</i> (G.Forst.) Copel.	New Zealand Islands; Perrie (WELT P20874)	DQ401117	DQ401127	DQ401122	-	-	-
<i>Microsorium pustulatum</i> (G.Forst.) Copel.	Mainland Australia: Victoria; CC.Chen 1081 (H)	MH051181	MH113480	MH113513	MH113546	MH113580	MH113613
<i>Microsorium pustulatum</i> (G.Forst.) Copel.	cult. RBGV; CC.Chen 1082 (H)	MH665083	MH665149	-	-	-	-
<i>Microsorium rubidum</i> (Kunze) Copel.	cult. KBCC K034174 [Malay Peninsula]; (H)	MH665084	MH665150	MH665214	-	-	-
<i>Microsorium rubidum</i> (Kunze) Copel.	Taiwan Islands; CC.Chen 1008 (H)	MH665085	MH665151	MH665215	MH665001	MH665015	MH665026
<i>Microsorium rubidum</i> (Kunze) Copel.	Indonesia Islands: Java; Wade 1931 (TAIF)	MH665086	MH665152	MH665216	-	-	-
<i>Microsorium scandens</i> (G.Forst.) Tindale	cult. BGG, Kreier s.n. (GOET)	DQ212057	DQ212058	DQ179641	-	-	-
<i>Microsorium scandens</i> (G.Forst.) Tindale	New Zealand Islands; Perrie et al. (WELT P20875)	DQ401118	DQ401128	DQ401123	-	-	-
<i>Microsorium scandens</i> (G.Forst.) Tindale	Mainland Australia: Victoria; CC.Chen 1080 (H)	MH051182	MH113481	MH113514	MH113547	MH113581	MH113614
<i>Microsorium scolopendria</i> (Burm. f.) Copel.	Taiwan Islands; CC.Chen 1085 (H)	MH051190	MH113489	MH113522	MH113555	MH113588	MH113622
<i>Microsorium scolopendria</i> (Burm. f.) Copel.	Taiwan Islands; CC.Chen 1009 (H)	MH665087	MH665153	MH665217	-	-	-
<i>Microsorium scolopendria</i> (Burm. f.) Copel.	cult. BGG; Schneider s.n. (GOET)	DQ642163	DQ642201	DQ642247	-	-	-
<i>Microsorium scolopendria</i> (Burm. f.) Copel.	Mayotte Island; Rakotonirainibe et al. 6601 (P)-1	DQ642164	DQ642202	DQ642248	-	-	-
<i>Microsorium scolopendria</i> (Burm. f.) Copel.	Mayotte Island; Rakotonirainibe et al. 6601 (P)-2	GQ256317	GQ256395	GQ256245	-	GQ256159	-
<i>Microsorium spectrum</i> (Kaulf.) Copel.	Hawaiian Islands; Wood 10936 (LOA)	EU482967	EU483018	EU483064	-	-	-
<i>Microsorium spectrum</i> (Kaulf.) Copel.	Hawaiian Islands; Hoshizaki 1350 (UC)	EU482968	EU483019	EU483065	-	-	-
<i>Microsorium steerei</i> (Harr.) Ching	Taiwan Islands; CC.Chen 1013 (H)	MH051183	MH113482	MH113515	MH113548	MH113582	MH113615

<i>Microsorium thailandicum</i> T. Booknerd & Noot.	cult. BGG; Schwertfeger s.n. (GOET)	EU482969	EU483020	EU483066	-	-	-
<i>Microsorium vieillardii</i> (Mett.) Copel.	cult. CAG; Smith s.n. (UC)	DQ179634	DQ179637	DQ179644	-	-	-
<i>Microsorium vieillardii</i> (Mett.) Copel.	cult. DBG; Schneider s.n. (GOET)	DQ179635	DQ179638	DQ179645	-	-	-
<i>Microsorium whiteheadii</i> A.R.Sm. & Hoshiz.	Sumatra Island; Whitehead s.n. (UC)	EU482970	EU483021	EU483067	-	-	-
<i>Neocheiropteris palmatopedata</i> (Baker) Christ	Mainland China: Yunnan province; Zhang 4482 (PE)	GQ256318	GQ256396	GQ256246	-	GQ256160	-
<i>Neocheiropteris palmatopedata</i> (Baker) Christ	cult. KBG; Kim 2012-1 (KUN)	JX103706	JX103748	JX103790	-	JX103664	-
<i>Neocheiropteris palmatopedata</i> (Baker) Christ	Mainland China; Schneider s.n. (BGUZ) (GOET)	AY362567	AY362640	-	-	-	-
	cult. BGG, Schneider s.n. (GOET)	-	-	DQ212059	-	-	-
	cult.; Schneider s.n. (GOET)	-	-	-	EF463833	EF463502	-
<i>Neocheiropteris palmatopedata</i> (Baker) Christ	Mainland China: Sichuan province; Kuo 1552 (TAIF)	MH051185	MH113484	MH113517	MH113550	MH113584	MH113617
<i>Neocheiropteris triglossa</i> (Baker) Ching	Mainland China: Yunnan province; W.M. Zhu 57112 (KUN)	HQ597010	-	HQ597019	-	HQ597024	-
<i>Neolepisorus ensatus</i> (Thunb.) Ching	Korean Peninsula; Zhang 3611 (PE)	GQ256319	GQ256397	GQ256247	-	GQ256161	-
<i>Neolepisorus ensatus</i> (Thunb.) Ching	Taiwan Islands; CC.Chen 1011 (H)	MH051184	MH113483	MH113516	MH113549	MH113583	MH113616
<i>Neolepisorus fortunei</i> (T.Moore) Li Wang	Mainland China: Yunnan province; Shui 80768 (PE)	-	GQ256393	GQ256243	-	GQ256157	-
<i>Neolepisorus fortunei</i> (T.Moore) Li Wang	cult. KBG, China; Kim 2012-5 (KUN)	JX103702	JX103744	JX103786	-	JX103660	-
<i>Neolepisorus fortunei</i> (T.Moore) Li Wang	Taiwan Islands; Ranker 2087 (COLO)	DQ642159	DQ642197	DQ642242	-	-	-
	Taiwan Islands; E. Schuettpelz 1074A (DUKE)	-	-	-	-	-	KF909024
<i>Neolepisorus fortunei</i> (T.Moore) Li Wang	Mainland China; Zhang 3446 (PE)	EU482955	EU483006	EU483052	-	-	-
<i>Neolepisorus fortunei</i> (T.Moore) Li Wang	Taiwan Islands; CC.Chen 1012 (H)	MH051186	MH113485	MH113518	MH113551	MH113585	MH113618
<i>Neolepisorus fortunei</i> (T.Moore) Li Wang	Taiwan Islands; CC.Chen 1096 (H)	-	MH665154	MH665218	-	-	-
<i>Neolepisorus ovatus</i> (Wall. ex Bedd.) Ching	Mainland China; Zhang 728-1 (PE)	EU482972	EU483023	EU483068	-	-	-
	Mainland China: Yunnan province, Yongren; X.Y.Du 0936 (KUN)	-	-	-	-	HQ597028	-
<i>Neolepisorus ovatus</i> (Wall. ex Bedd.) Ching	Mainland China: Hubei province; CC.Chen 1041 (H)	MH051187	MH113486	MH113519	MH113552	MH113586	MH113619
<i>Neolepisorus ovatus</i> (Wall. ex Bedd.) Ching	Mainland China: Sichuan province; Kuo 2171 (TAIF)	MH665088	MH665155	MH665219	-	-	-
	Mainland China: Yunnan province; Shui YM et al. 80898	-	-	-	-	KX891395	-
<i>Neolepisorus phyllomanes</i> (Christ) Ching	cult. RBGE; Nicholson s.n. (E)	EU482973	EU483024	EU483069	-	-	-
<i>Neolepisorus zippelii</i> (Blume) L. Wang	Indonesia Islands: Java; Tsutsumi IN112 (TI)	AB232411	DQ642203	DQ642249	-	-	-
<i>Neolepisorus zippelii</i> (Blume) L. Wang	Indonesia Islands: Java; Wade 1794 (TAIF)	MH051188	MH113487	MH113520	MH113553	MH175523	MH113620
<i>Neolepisorus sp.</i>	Mainland China: Chongqing; Wei R WR147 (PE)	KX891380	KX891399	KX891367	-	KX891396	-
<i>Paragramma longifolia</i> (Blume) T. Moore	Malay Peninsula; Cranfill BF012 (UC)	DQ642157	DQ642195	DQ642239	-	-	-
	cult. BGM; Schneider s.n. (GOET)	-	-	-	EF463825	EF463497	-
<i>Platygyria x inaequibasis</i> Ching & S.K. Wu	Tibetan Plateau; Zhang 4615 (PE)	GQ256320	GQ256398	GQ256248	-	GQ256162	-
<i>Platygyria soulieana</i> (Christ) X.C. Zhang & Q.R. Liu	Mainland China: Sichuan province; Zhang 5168 (PE)	GQ256321	GQ256399	GQ256249	-	GQ256163	-
<i>Platygyria waltonii</i> (Ching) Ching and S.K. Wu	Tibetan Plateau; Zhang 4639 (PE)	GQ256322	GQ256400	GQ256250	-	GQ256164	-
<i>Platygyria waltonii</i> (Ching) Ching and S.K. Wu	Mainland China; Cranfill 94-266-29 (UC)	EU482944	EU482994	U483039	-	-	-
<i>Thylacopteris papillosa</i> (Blume) J.Sm.	Indonesia Islands: Java; Gravendeel et al. 559 (L)	AY459175	AY459188	AY459183	EF463856	EF463518	-
<i>Thylacopteris papillosa</i> (Blume) J.Sm.	Borneo Island; Daniele Cicuzza 2258 (UBDH)	MH665089	MH665156	MH665220	MH665002	MH665016	-
<i>Tricholepidium normale</i> (D. Don) Ching	Yunnan; Shui 80596 (PE)	GQ256323	GQ256401	GQ256251	-	-	-
	cult. KBG; X.Y.Du 1004 (KUN)	-	-	-	-	HQ597025	-
<i>Tricholepidium normale</i> (D. Don) Ching	Indochina: Vietnam; Wade 2649 (TAIF)	MH175520	MH113490	MH113523	MH113556	MH113589	MH113623
<i>Tricholepidium normale</i> (D. Don) Ching	Indochina: Vietnam; Wade 4101 (TAIF)	MH665090	MH665157	MH665221	MH665003	MH665017	MH665027
<i>Aglaomorpha meyeniana</i> Schott	cult. Goettingen; Janssen 2260 (GOET)	AY529153	-	-	-	-	-
	cult. Goettingen; Janssen V-17 (GOET)	-	AY459185	-	-	-	-
	cult. KBCC K016952	-	-	FJ807657	JF304020	-	JF303958
<i>Polypodium glycyrrhiza</i> D.C. Eaton	Canada: Squamish-Lilloet; Rothfels 4086 (DUKE)	KP136832*	-	KP136832*	KP136832*	KP136832*	KP136832*
	cult. BGG; Schwertfeger s.n. (GOET)	-	FJ825671	-	-	-	-
<i>Pyrrosia polydactyla</i> (Hance) Ching	Taiwan Islands; Ranker 2080 (COLO)	EF463259	-	-	EF463844	EF463511	-
	Taiwan Islands; Knapp 3801 (P)	-	KY931286	KY931410	-	-	-
	Taiwan Islands; Lu PF 21430 (PE)	-	-	-	-	-	KY633008

Outgroup

Outgroup

Outgroup

Table 2. List of primers for amplifying the gene regions used in this study.

Gene	Primer	Direction	Sequence	Reference
rbcL	F1	Forward	ATGTCACCACAAACGGAGAC	Li, C., Lu, S. & Yang, Q. (2004)
	rbcL341F	Forward	CCTTCGAATTCCTCCCGCTT	This study
	aF	Forward	ATGTCACCACAAACAGAGACTAAAGC	Hasebe et al. (1994)
	R1379	Reverse	GCAGCTAATTCAGGACTCC	Li, C., Lu, S. & Yang, Q. (2004)
	rbcL1105R	Reverse	TCGGTTAGAGCAGGCATGTG	This study
	cR	Reverse	GCAGCAGCTAGTTCCGGGCTCCA	Hasebe et al. (1994)
	aR	Reverse	CTTCTGCTACAAATAAGAATCGATCTCTCCA	Hasebe et al. (1994)
rps4+rps4-trnS	rps4F	Forward	ATGTCSCGTTAYCGAGGACCT	Small et al. (2005)
	trnS	Reverse	TACCGAGGGTTTCGAATC	Schneider et al. (2005)
trnL+trnL-trnF	trnLfern1	Forward	GGCAGCCCCCARATTCAGGGRAACC	Trewick et al. (2002)
	trnFf	Reverse	ATTTGAACTGGTGACACGAG	Taberlet et al. (1991)
	trnLd	Reverse	GGGGATAGAGGGGACTTGAAC	Taberlet et al. (1991)
atpA	ESATPF412F	Forward	GARCARGTTCGACAGCAAGT	Schuettpelz et al. (2006)
	ESATPA557R	Reverse	ATTGTATCTGTAGCTACTGC	Schuettpelz et al. (2006)
	ESATPA877R	Reverse	CATCTCCCGGATATGCTTCTCG	Schuettpelz et al. (2006)
atpB	ESATPB172F	Forward	AATGTTACTTGTGAAGTWCAACAAT	Schuettpelz & Pryer (2007)
	ATPB910R	Reverse	TTCCTGYARAGANCCCATTTCTGT	Schuettpelz & Pryer (2007)
matK	PolypodF1	Forward	ATTTYTGGARGAYAGAYTDCC	Proposed by the CBoL Plant Barcoding
	PolypodF2	Forward	AATTCRCARTCYAYYCATT	Working group (http://www.boldsystems.org/index.php/Public_Primer_PrimerSearch)
	PolypodR1	Reverse	CGTRGTATATATCTCRATYTACGC	

Table 3 Best-fitting models and parameter values of large and small dataset for separate genes of rbcL, rps4 & rps4- trnS IGS, trnL-trnF region, atpA, atpB & rbcL-atpB IGS, and matK.

DNA regions	Large dataset				Small dataset			
	Selected model	taxa	sites	Constant sites	Selected model	taxa	sites	Constant sites
rbcL	BIC: TIM2e+R4	308	1237	66%	BIC: TIM2e+R3	49	1237	78%
rps4 + rps4- trnS	BIC: TVM+R4	310	1169	45%	BIC: K3Pu+G4	50	1044	50%
trnL + trnL-trnF	BIC: TVM+R4	302	1088	42%	BIC: K3Pu+R3	49	931	50%
atpA	BIC: TIM+I+G4	64	1023	72%	BIC: TIM3+G4	45	1013	73%
rbcL-atpB + atpB *	BIC: GTR+I+G4	185	1584	68%	BIC: TNe+R2	47	676	76%
matK	BIC: TVM+R3	53	834	43%	BIC: TVM+R3	40	834	44%
six-combination	BIC: GTR+R5	316	6935	57%	BIC: GTR+R4	50	5735	62%
four-combination	BIC: TVM+R5	316	5078	57%	-	-	-	-
three-combination	BIC: TVM+R5	316	3494	51%	-	-	-	-

* atpB & rbcL-atpB are analysed in large dataset, and atpB was analysed in small dataset.

Table 4 The proposed generic names, following the status of the name based on the Tropicos database (tropicos.org), type species & if it is included in this study. Group indicates the clade that the type species of the genus belongs to; Mono indicates if the genus is monophyletic or not, and an asterisk * that only one species is included in this study; the last column shows original and lectotype publications. Names in bold used in this study. Abbreviations: leg., legitimate; nom. cons., conserved name; nom. rej., name rejected; illeg. hom., name illegitimate due to homonymy; LT, lectotype; -, lack of data.

generic names	Status	Type species/Included	Groups	Mono	publications
<i>Belvisia</i> Mirbel	nom. rej.	[LT] <i>Belvisia spicata</i> (L. f.) Mirb. ex Copel. ≡ <i>Lepisorus spicatus</i> (L.f.) Li Wang	Yes <i>Lepisorus</i>	Yes	Hist. Nat. Vég. 3: 473; 5: 111. 1803. [LT] Gen. Fil.: 192. 1947.
<i>Bosmania</i> Testo	leg.	<i>Bosmania membranacea</i> (D. Don) Testo ≡ <i>Microsorium membranaceum</i> (D. Don) Ching	Yes MG1	Yes	Syst. Bot. 44: 1-16. 2019.
<i>Caobangia</i> A.R.Sm. & X.C.Zhang	leg.	<i>Caobangia squamata</i> A.R.Sm. & X.C.Zhang ≡ <i>Lemmaphyllum squamatum</i> (A.R.Sm. & X.C.Zhang) Li Wang	Yes <i>Lemmaphyllum</i>	Yes*	Novon 12: 546–549, f. 1. 2002.
<i>Christiopteris</i> Copel.	leg.	<i>Christiopteris sagitta</i> (Christ) Copel. ≡ <i>Aglaomorpha sagitta</i> (Christ) Hovenkamp & S.Linds	No -	-	Fragm. Fl. Philipp.: 188. 1905.
<i>Colysis</i> C. Presl	-	[LT] <i>Colysis hemionitidea</i> (Wall. Ex Mett.) C. Presl ≡ <i>Leptochilus hemionitideus</i> (C. Presl) Noot.	Yes <i>Leptochilus</i>	No	Epim. Bot.: 146. 1849. [LT] Index Filic., Suppl. 3: 12. 1934.
<i>Dendroconche</i> Copel.	leg.	<i>Dendroconche annabellae</i> (H.O. Forbes) Copel. = <i>Microsorium linguiforme</i> (Mett.) Copel.	Yes MG3	Yes	Philipp. J. Sci., C. 6: 91. 1911.
<i>Dendroglossa</i> C. Presl	-	[LT] <i>Dendroglossa normalis</i> C. Presl. ≡ <i>Leptochilus minor</i> Fée	No -	No	Epim. Bot.: 149. 1849. [LT] Gen. Fil.: 199. 1947.
<i>Diblemma</i> J. Smith	leg.	<i>Diblemma samarensis</i> J. Sm. ≡ <i>Microsorium samarense</i> (J. Sm.) Bosman	No -	-	J. Bot. (Hooker). 3: 399. 1841.
<i>Dictymia</i> J. Smith	leg.	<i>Dictymia attenuata</i> (R. Br.) J. Sm.	No -	-	Bot. Mag. 72(Comp.): 16. 1846.
<i>Drymotaenium</i> Makino	nom. rej.	<i>Drymotaenium miyoshianum</i> (Makino) Makino. = <i>Lepisorus miyoshianus</i> (Mak.) Fraser-Jenk. &	Yes <i>Lepisorus</i>	Yes*	Bot. Mag. (Tokyo). 15(174): 102. 1901.

Subh. Chande

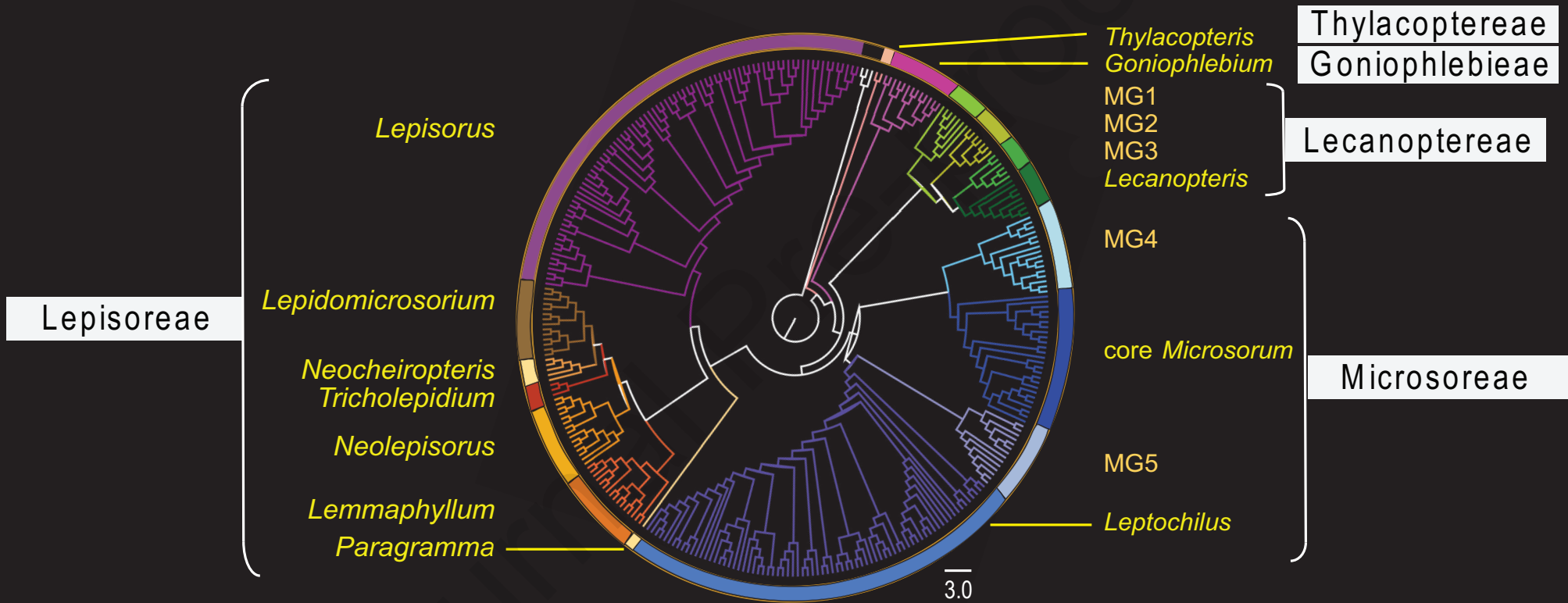
Goniophlebium (Blume) C. Presl	leg.	[LT] <i>Goniophlebium subauriculatum</i> (Blume) C. Presl	Yes	<i>Goniophlebium</i>	Yes	Tent. Pterid.: 186. 1836. [LT] Taxon 39: 105. 1990.
<i>Kaulinia</i> B.K. Nayar	-	<i>Kaulinia pteropus</i> (Blume) B.K. Nayar ≡ <i>Microsorium pteropus</i> (Blume) Copel.	Yes	<i>Leptochilus</i>	No	Taxon 13: 67. 1964.
<i>Kontumia</i> S.K.Wu & K.L.Phan	-	<i>Kontumia heterophylla</i> S.K. Wu & K.L. Phan = <i>Leptochilus heterophylla</i> (S.K. Wu & K.L. Phan) Christenh.	Yes	<i>Leptochilus</i>	Yes*	Novon 15(1): 245–247, f. 1, 2. 2005.
Lecanopteris Reinw.	leg.	<i>Lecanopteris carnosa</i> (Reinw.) Blume	Yes	<i>Lecanopteris</i>	Yes	Flora 8(2, Beil.): 48. 1825.
Lemmaphyllum C.Presl	leg.	[LT] <i>Lemmaphyllum spatulatum</i> C. Presl = <i>Lemmaphyllum carnosum</i> (Hook.) C. Presl	Yes	<i>Lemmaphyllum</i>	Yes	Epim. Bot.: 157. 1849. [LT] Gen. Fil.: 189. 1947.
<i>Lepidogrammitis</i> Ching	-	<i>Lepidogrammitis drymoglossoides</i> (Baker) Ching = <i>Lemmaphyllum drymoglossoides</i> (Baker) Ching	Yes	<i>Lemmaphyllum</i>	No	Sunyatsenia 5(4): 258. 1940.
Lepidomicrosorium Ching & K.H.Shing	leg.	<i>Lepidomicrosorium subhastatum</i> (Baker) Ching = <i>Lepidomicrosorium buergerianum</i> (Miq.) Ching & K.H. Shing	Yes	<i>Lepidomicrosorium</i>	Yes	Bot. Res. Academia Sinica. 1:1. 1983.
Lepisorus (J.Sm.) Ching	nom. cons.	<i>Lepisorus nudus</i> (Hook.) Ching	No	-	Yes	Bull. Fan Mem. Inst. Biol. 4: 47. 1933.
Leptochilus Kaulf.	leg.	<i>Leptochilus axillaris</i> (Cav.) Kaulf.	Yes	<i>Leptochilus</i>	Yes	Enum. Filic. 147, pl. 1, f. 10. 1824.
<i>Metapolypodium</i> Ching	leg.	<i>Metapolypodium manmeiense</i> (Christ) Ching ≡ <i>Goniophlebium manmeiense</i> (Christ) Rödl-Linder	Yes	<i>Goniophlebium</i>	Yes	Acta Phytotax. Sin. 16(4): 28. 1978.
Microsorium Link	leg.	<i>Microsorium irregulare</i> Link = <i>Microsorium punctatum</i> (L.) Copel.	Yes	core <i>Microsorium</i>	No	Hort. Berol. 2: 110. 1833.
<i>Myrmecophila</i> (H.Christ) ex Nakai	illeg. hom.	<i>Myrmecophila sinuosa</i> (Hook.) Nakai ex H. Itô. ≡ <i>Lecanopteris sinuosa</i> (Hook.) Copel.	Yes	<i>Lecanopteris</i>	Yes*	Bot. Mag. (Tokyo). 43: 6. 1929.
<i>Myrmecopteris</i> Pichi Serm.	-	<i>Myrmecopteris sinuosa</i> (Wall. ex Hook.) Pic. Serm. ≡ <i>Lecanopteris sinuosa</i> (Wall. ex Hook.) Copel.	Yes	<i>Lecanopteris</i>	No	Webbia 31: 239. 1977.

<i>Myuropteris</i> C. Chr.	-	<i>Myuropteris cordata</i> (Christ) C. Chr. = <i>Leptochilus cantoniensis</i> (Baker) Ching	Yes	<i>Leptochilus</i>	Yes*	Dansk Bot. Ark. 6(3): 73. 1929.
<i>Neocheiropteris</i> H. Christ	leg.	<i>Neocheiropteris palmatopedata</i> (Baker) Christ	Yes	<i>Neocheiropteris</i>	Yes	Bull. Soc. Bot. France: Mem. 1: 21. 1905.
<i>Neolepisorus</i> Ching	leg.	<i>Neolepisorus ensatus</i> (Thunb.) Ching	Yes	<i>Neolepisorus</i>	Yes	Bull. Fan Mem. Inst. Biol., Bot. 10(1): 11–12. 1940.
<i>Nistarika</i> B.K. Nayar, Madhus. & Molly	-	<i>Leptochilus axillaris</i> (Cav.) Kaulf.	Yes	<i>Leptochilus</i>	No*	Fern Gaz. 13(1): 33, f. 1–6. 1985.
<i>Paragramma</i> (Blume) T.Moore	nom. rej.	[LT] <i>Paragramma longifolia</i> (Blume) T. Moore	Yes	<i>Paragramma</i>	Yes	Index Fil. xxxii. 1857. [LT] Hist. Fil.: 114. 1875
<i>Paraleptochilus</i> Copel.	-	<i>Paraleptochilus decurrens</i> (Blume) Copel. ≡ <i>Leptochilus decurrens</i> Blume	Yes	<i>Leptochilus</i>	No*	Gen. Fil. 198, t. 7. 1947.
<i>Phymatosorus</i> Pic.Serm.	leg.	<i>Phymatosorus scolopendria</i> Pichi Serm. ≡ <i>Microsorium scolopendria</i> (Burm. f.) Copel.	Yes	core <i>Microsorium</i>	No	Webbia 28: 457. 1973.
<i>Platygyria</i> Ching & S.K.Wu	-	<i>Platygyria waltonii</i> (Ching) Ching & S.K. Wu. ≡ <i>Lepisorus waltonii</i> (Ching) S.L.Yu	Yes	<i>Lepisorus</i>	Yes	Acta Bot. Yunnan. 2(1): 67–68. 1980.
<i>Podosorus</i> Holttum	-	<i>Podosorus angustatus</i> Holttum	No	-	-	Kew Bull. 20: 455. 1966.
<i>Polypodiastrium</i> Ching	leg.	<i>Polypodiastrium argutum</i> (Wall. ex Hook.) Ching. ≡ <i>Goniophlebium argutum</i> (Wall. ex Hook.) J. Sm.	Yes	<i>Goniophlebium</i>	Yes	Acta Phytotax. Sin. 16(4): 27–28. 1978.
<i>Polypodiodes</i> Ching	leg.	<i>Polypodiodes amoena</i> (Wall. ex Mett.) Ching ≡ <i>Goniophlebium amoenum</i> (Wall. ex Mett.) Bedd.	Yes	<i>Goniophlebium</i>	Yes	Acta Phytotax. Sin. 16(4): 26–27. 1978.
<i>Schellolepis</i> J.Sm.	-	[LT] <i>Schellolepis verrucosa</i> (Wall. ex Hook.) J. Sm. = <i>Goniophlebium percussum</i> (Cav.) Wanger & Grether	No	-	-	Ferns Brit. For.: 82. 1866. [LT] Hist. Fil.: 93. 1875.
<i>Thylacopteris</i> Kunze ex J. Smith	-	<i>Thylacopteris papillosa</i> (Blume) J. Sm.	Yes	<i>Thylacopteris</i>	Yes*	Hist. Fil. 87. 1875.
<i>Tricholepidium</i> Ching	leg.	<i>Tricholepidium normale</i> (D. Don) Ching	Yes	<i>Tricholepidium</i>	Yes*	Acta Phytotax. Geobot. 29(1–5): 41. 1978.
<i>Weatherbya</i> Copel.	-	<i>Weatherbya accedens</i> (Blume) Copel. = <i>Lepisorus accedens</i> (Blume) Hosok.	Yes	<i>Lepisorus</i>	Yes*	Gen. Fil. 191. 1947.
<i>Zealandia</i> Testo & A. R. Field	leg.	<i>Zealandia pustulata</i> (G. Forst.) Testo&A. R. Field ≡ <i>Microsorium pustulatum</i> (G. Forst.) Copel.	Yes	MG2	Yes	Syst. Bot. 44: 1-16. 2019.

Table 5 List of generic name and grouping of the microsoroid ferns in selected taxonomic and phylogenetic works. Abbreviations: GO, goniophlebioid clade; LC, lecanopteroid clade; LP, lepisoroid clade; ME, membranaceoid clade; MI, microsoroid s.s. clade; TH, thylacopteroid clade; Sf.LO, Subfamily Loxogrammoideae; Sf.DN, Subfamily Drynarioideae; Sf.MI, Subfamily Microsoroideae; T.PO, Tribe Polypodieae; T.LP, Tribe Lepisoreae; T.MI, Tribe Microsoreae; T.GO, Goniophlebieae; T.TH, Thylacopterae; T.LC, Lecanopterae.

The previously proposed generic names and grouped in this study		Hennipman et al. (1990)		Kreier et al. (2008)		PPGI (2016)	
<i>Goniophlebium</i>	T.GO	<i>Polypodium-Goniophlebium</i> Group	T.PO	<i>Goniophlebium</i>	GO	<i>Goniophlebium</i>	Sf.MI
<i>Metapolypodium</i>	T.GO			<i>Goniophlebium</i>	GO	<i>Goniophlebium</i>	Sf.MI
<i>Polypodiastrium</i>	T.GO			<i>Goniophlebium</i>	GO	<i>Goniophlebium</i>	Sf.MI
<i>Polypodiodes</i>	T.GO			<i>Goniophlebium</i>	GO	<i>Goniophlebium</i>	Sf.MI
<i>Schellolepis</i>	T.GO	<i>Polypodium-Goniophlebium</i> Group	T.PO	<i>Goniophlebium</i>	GO		
<i>Thylacopteris</i>	T.TH	<i>Thylacopteris</i>	T.PO	<i>Thylacopteris</i>	TH	<i>Thylacopteris</i>	Sf.MI
<i>Lepisorus</i>	T.LP	<i>Lepisorus</i>	T.LP	<i>Lepisorus</i>	LP	<i>Lepisorus</i>	Sf.MI
<i>Paragramma</i>	T.LP	<i>Lepisorus</i>	T.LP	<i>Lepisorus</i>	LP	<i>Paragramma</i>	Sf.MI
<i>Belvisia</i>	T.LP	<i>Belvisia</i>	T.LP	<i>Belvisia</i>	LP	<i>Lepisorus</i>	Sf.MI
<i>Drymotaenium</i>	T.LP	<i>Drymotaenium</i>	T.LP	<i>Drymotaenium</i>	LP	<i>Lepisorus</i>	Sf.MI
<i>Lemmaphyllum</i>	T.LP	<i>Lemmaphyllum</i>	T.LP	<i>Lemmaphyllum</i>	LP	<i>Lemmaphyllum</i>	Sf.MI
<i>Caobangia</i>	T.LP					<i>Lemmaphyllum</i>	Sf.MI
<i>Lepidogrammitis</i>	T.LP	<i>Lemmaphyllum</i>	T.LP	<i>Lepidogrammitis</i>	LP	<i>Lemmaphyllum</i>	Sf.MI
<i>Weatherbya</i>	T.LP	<i>Lemmaphyllum</i>	T.LP	<i>Lemmaphyllum</i>	LP	<i>Lemmaphyllum</i>	Sf.MI
<i>Lecanopteris</i>	T.LC	<i>Lecanopteris</i>	T.MI	<i>Lecanopteris</i>	LC	<i>Lecanopteris</i>	Sf.MI
<i>Myrmecophila</i>	T.LC	<i>Lecanopteris</i>	T.MI	<i>Lecanopteris</i>	LC		

<i>Myrmecopteris</i>	T.LC	<i>Lecanopteris</i>	T.MI				
<i>Colysis</i>	T.MI	<i>Colysis</i>	T.MI	<i>Leptochilus</i>	MI	<i>Leptochilus</i>	Sf.MI
<i>Dendroglossa</i>	T.MI	<i>Colysis</i>	T.MI				
<i>Myuropteris</i>	T.MI	<i>Colysis</i>	T.MI				
<i>Paraleptochilus</i>	T.MI	<i>Colysis</i>	T.MI	<i>Leptochilus</i>	MI		
<i>Leptochilus</i>	T.MI	<i>Leptochilus</i>	T.MI	<i>Leptochilus</i>	MI	<i>Leptochilus</i>	Sf.MI
<i>Kontumia</i>	T.MI					<i>Leptochilus</i>	Sf.MI
<i>Nistarika</i>	T.MI	<i>Leptochilus</i>	T.MI				
<i>Microsorium</i>	T.MI	<i>Microsorium</i>	T.MI	<i>Microsorium</i>	MI, ME, LC	<i>Microsorium</i>	Sf.MI
<i>Diblemma</i>	T.MI	<i>Microsorium</i>	T.MI				
<i>Dendroconche</i>	T.MI	<i>Microsorium</i>	T.MI	<i>Microsorium</i>	LC	<i>Microsorium</i>	Sf.MI
<i>Kaulinia</i>	T.MI	<i>Microsorium</i>	T.MI			<i>Microsorium</i>	Sf.MI
<i>Podosorus</i>	T.MI	<i>Microsorium</i>	T.MI				
<i>Neocheiropteris</i>	T.LP	<i>Neocheiropteris</i>	T.MI	<i>Neocheiropteris</i>	LP	<i>Neocheiropteris</i>	Sf.MI
<i>Neolepisorus</i>	T.LP	<i>Neocheiropteris</i>	T.MI	<i>Neolepisorus</i>	LP	<i>Neolepisorus</i>	Sf.MI
<i>Tricholepidium</i>	T.LP	<i>Neocheiropteris</i>	T.MI	<i>Tricholepidium</i>	LP	<i>Tricholepidium</i>	Sf.MI
<i>Lepidomicrosorium</i>	T.LP			<i>Microsorium</i> <i>Neocheiropteris</i> <i>Lepidomicrosorium</i>	LP	<i>Lepidomicrosorium</i>	Sf.MI
<i>Phymatosorus</i>	T.MI	<i>Phymatosorus</i>	T.MI	<i>Phymatosorus</i>	MI	<i>Microsorium</i>	Sf.MI
<i>Platygyria</i>	T.LP	<i>Neocheiropteris</i>	T.MI	<i>Lepisorus</i>	LP		
<i>Dictymia</i>	-	<i>Dictymia</i>	T.MI			<i>Dictymia</i>	Sf.LO
<i>Christiopteris</i>	-	<i>Christiopteris</i>	T.MI			<i>Aglaomorpha</i>	Sf.DN



Highlights

- The microsoroid ferns comprise up to 17 genera.
- Five tribes have been identified.
- A large sampling (over 70% species) and up to six chloroplast DNA regions have been used.
- The DNA regions *matK* and *atpA* are useful to improve the phylogenetic hypotheses of the microsoroid ferns.